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**Big whirls have little whirls that feed on their velocity  
and little whirls have lesser whirls and so on to viscosity  
(Richardson 1926)**



UNIVERSITY OF ALBERTA

THE EFFECTS OF SOLAR RADIATION AND WATER COLUMN MIXING ON THE  
PHYTOPLANKTON OF BOREAL LAKES

by

**Marguerite Agnes Xenopoulos**



A thesis submitted to  
the Faculty of Graduate Studies and Research  
in partial fulfillment of the requirements for the degree of  
DOCTOR OF PHILOSOPHY

IN

ENVIRONMENTAL BIOLOGY AND ECOLOGY

DEPARTMENT OF BIOLOGICAL SCIENCES

EDMONTON, ALBERTA

SPRING 2002





# **University of Alberta**

## **Faculty of Graduate Studies and Research**

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled “The effects of solar radiation and water column mixing on the phytoplankton of boreal lakes” submitted by Marguerite Agnes Xenopoulos in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the field of Environmental Biology and Ecology.



**To my grandmothers,  
Margarita Delatolla and Agnes Xenopoulos**





## ABSTRACT

I examined the combined effects of high ultraviolet radiation (UVR) and shallow, secondary, near-surface thermoclines on the phytoplankton of boreal lakes. My objectives were: 1) to investigate the frequency that near-surface thermoclines occur in lakes of different size and water clarity and their role in the exposure of plankton to UVR; 2) to compare phytoplankton biomass, production, growth rates and elemental composition under different solar radiation regimes (Photosynthetically Active Radiation (PAR) only, PAR+UVA, and PAR+UVA+UVB), phosphorus concentrations and restricted mixing conditions; and 3) to determine the interactive effects of elevated UVR exposure, temperature and mixing on the phytoplankton pigments in lakes differing in important physico-chemical characteristics. This study was conducted in several lakes of the boreal forest at the Experimental Lakes Area (ELA; northwestern Ontario, Canada). A comparative survey allowed for establishment of relationships between near-surface thermoclines, plankton abundance, primary production, pigment concentration and UVR-related environmental conditions. I also used experiments to test the influence of UVR on algal growth kinetics, elemental composition, biomass and production, under very low mixing conditions. Survey results obtained using 30 years of archived data show that near-surface thermoclines can occur on 90% of summer days in small lakes of the ELA and up to 40% in larger lakes from the Northwest Ontario Lake Size Series (Ontario). Field results (from 1998 & 1999) indicate that planktonic concentrations of pigments from chrysophytes and total algae were negatively correlated with UVB exposure ( $r^2=0.57$  and  $r^2=0.64$ , respectively) in slightly stained lakes but not in clear lakes. Planktonic concentration of pigments from chlorophytes, dinoflagellates and Cyanobacteria were generally positively related with UVB exposure particularly during low mixing conditions. Near-surface phytoplankton growth rates were reduced by 23-87% in treatments exposed to UVA and UVB compared to PAR only treatments. However phytoplankton growth was co-regulated by P-limitation and UVR with highest growth rates found in high P, low





UVR treatments. Phytoplankton that originated from the bottom of the mixed layer had in most cases reduced chlorophyll and photosynthesis when exposed to near-surface UVR but algae that originated from the surface were generally unaffected by UVR exposure. Together these results demonstrate the importance of considering mixing and interactions with other factors in UVR studies of phytoplankton.



## PREFACE TO THE THESIS

The structure of this thesis follows the paper format outlined by the Faculty of Graduate Studies and Research, University of Alberta, 2001. The research is presented in five manuscripts, chapters 2 through 6. The introductory and concluding chapters are intended to outline the research, summarize the findings and present areas of future research. I have acknowledged individuals that have contributed their ideas or time in the collection of data by way of authorship and used the plural throughout the data chapters. Although I have made an effort to keep repetition to a minimum, common aspects that underlie the research are unavoidably repeated. Below is a list of manuscripts resulting from the five chapters as they have been, or I expect them to be published.

**Chapter 2:** Xenopoulos, M.A. and Schindler D.W. 2001. Physical Factors Determining UV Flux into Ecosystems. *In* Ecosystems, Evolution and Ultraviolet Radiation, pp. 36-62. C.S. Cockell and A.R. Blaustein, editors, Springer-Verlag, New York.

**Chapter 3:** Xenopoulos, M.A. and Schindler, D.W. The environmental control of near-surface thermoclines in boreal lakes. *Ecosystems*, in press (accepted May 2001).

**Chapter 4:** Xenopoulos, M.A., Frost, P.C., and Elser, J.J. Joint effects of ultraviolet radiation and phosphorus supply on phytoplankton growth rate and elemental composition. *Ecology*, in press (accepted March 2001).

**Chapter 5:** Xenopoulos, M.A. and Schindler, D.W. Differential responses to UVR by bacterioplankton and phytoplankton from the surface and base of the mixed layer, submitted to *Freshwater Biology* (September 2001).

**Chapter 6:** Xenopoulos, M.A., Leavitt, P.R. and Schindler, D.W. Seasonal regulation of boreal lake phytoplankton by UV radiation: evidence from algal pigments. (manuscript).





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## 1. GENERAL INTRODUCTION

Solar radiation in aquatic ecosystems controls biological production, thermal stratification, water column mixing and the vertical distribution of organisms. Intense solar radiation during near-windless condition isolates water at the surface of the lake and potentially exposes plankton to the most harmful rays of sunlight (ultraviolet radiation, UVR) for prolonged periods. The objective of this study is to determine how phytoplankton is affected by the combined effects of high light, in particular ultraviolet-B (UVB) radiation and near-surface thermoclines (restricted, shallow mixing).

### **Effects of Increased UVR on Freshwater Biota**

As the result of decreasing ozone concentration in the global stratosphere, significant increases in UVB radiation reaching the earth's surface are now being recorded in north temperate latitudes where freshwater ecosystems are abundant (Stolarski et al. 1992; Kerr and McElroy 1993; Madronich et al. 1995; Xenopoulos and Schindler 2001). Ambient UVB can damage all planktonic organisms including phytoplankton (Smith et al. 1992; Karentz et al. 1994; Vernet 2000; Xenopoulos et al. 2000; Xenopoulos et al., in press), microbial food webs (Herndl et al. 1993; Jeffrey et al. 1996; Sommaruga et al. 1997, 1999; Xenopoulos and Bird 1997; Jeffrey et al. 2000) and zooplankton (Bidigare 1989; Williamson 1995; Zagarese and Williamson 2000; Leech and Williamson 2001). Studies have also shown that UVB can affect several processes at the ecosystem level such as community succession (Vinebrooke and Leavitt 1999; Xenopoulos et al. 2000), carbon flow (Mostajir et al. 2000) and trophic interactions (Bothwell et al. 1994).

In addition to the depleting stratospheric ozone, interactions among climate warming, drought, and acidification cause declines in the concentration and structure of dissolved organic carbon (DOC) in boreal lakes, which increases exposure of freshwater communities to all wavelengths of UVR and photosynthetically active radiation (PAR) (Schindler et al. 1996a, b; Williamson et al. 1996; Yan et al. 1996; Dillon and Molot 1997; Donahue et al. 1998). Boreal lakes are thus particularly vulnerable to increases in UVB, UVA and PAR penetration, as they are under a three-pronged attack from the complex interactions of climate warming, acidification and stratospheric ozone depletion (Gorham 1996).





Despite two decades of intensive UVR studies on freshwater, little is known about how mixing will potentially mediate exposure and damage by UVR as this physical aspect of lakes is not easily modeled. Furthermore, there is a need to study UVB and UVA and its interaction with other ecological factors (e.g., nutrients and temperature) particularly in light of recent connections established between multiple stressors (Schindler et al. 1996a; Frost et al. 1999; Leavitt et al. 1999; Hessen and Alstad Rukke 2000). For example, phosphorus concentrations (an important nutrient in boreal lakes, Schindler 1977) may influence responses of biota to high levels of UVR (Vernet 2000; Xenopoulos et al. in press). The few studies that have examined the additive interactions of multiple environmental stressors (e.g. pollutants, climate change, nutrients, temperature, acid rain) and UVR on aquatic ecosystems show that the combined effects may be much more severe than their individual effects. Given the rate of human-induced global change, many of these stressors are expected to become significant forces in aquatic systems in the coming years.

### **UVR effects in near-surface thermoclines**

Thermal structure and mixing in lakes can vary considerably from one day to another (Imberger and Patterson 1990). This variation affects the average light intensity experienced by the phytoplankton. Near-surface thermoclines are a common feature of lakes. They form above the main thermocline under hot, bright and near-windless conditions (Imberger 1985) and can retain the phytoplankton and bacterioplankton at shallow depths under extreme irradiances (Vincent et al. 1984; Milot-Roy and Vincent 1994; Xenopoulos et al. 2000). Near-surface thermoclines isolate the upper part of the epilimnion for hours and can be as shallow as 0.3-1.0 m (Imberger and Patterson 1990; Xenopoulos 1997; ELA records unpublished). They form during the day and are generally eroded at night by convective cooling (Imberger 1985), although some can persist for several days.

Near-surface thermoclines have the potential to increase UVR exposure to values that have negative effects. For example, Xenopoulos et al. (2000) found significant changes in species composition of the algal community when shallow surface thermoclines and high incident UVR co-occurred. In addition, when the epilimnion remained less than 2 meters deep there was a strong negative relationship between UVB and phytoplankton biomass. The community shifted from one dominated by chrysophytes and diatoms to one dominated by Cyanobacteria. This community shift was accompanied by a decrease in chlorophyll *a* by ~65% during a several day



period of very low wind and shallow surface stratification. In another study, Montecino et al. (1997) showed that the surface mixed layer of an Andean lake was shallower during high irradiance. This could potentially be devastating for a phytoplankton cell exposed to high irradiances when trapped in shallow mixing depths.

Here, I further investigate the interactive effects of UVR and lake mixing in a series of lakes of different size and clarity. The work was conducted at the Experimental Lakes Area (ELA) in northwestern Ontario, where small lakes vary greatly in optical properties and hence, potential UV penetration (Schindler 1971; Donahue et al. 1998).

## **Objectives**

My specific objectives are:

1. To investigate the physical factors affecting UVR flux into ecosystems (chapter 2)
2. To determine the effect of lake size, water transparency and wind on the development of near-surface thermoclines in boreal lakes using 30 years of archived data for lakes ranging in size from 2 to 8 000 000 ha (chapter 3).
3. To determine the interaction of phosphorus and UVR on the phytoplankton growth rate and elemental composition in shallow restricted mixing conditions (chapter 4).
4. To compare the sensitivities and acclimation responses to UVR of phytoplankton and bacterioplankton from the surface and base of the mixed layer under restricted mixing conditions (chapter 5).
5. To examine the short and long-term responses of phytoplankton to UVR and restricted mixing under natural conditions (chapter 6).

## **Proposed experiments**

I achieved the aforementioned objectives in three ways: First a review of the literature (chapter 2) was done to investigate the factors that affect the amount of UVR that reaches the Earth's surface and penetrates into lakes. Second, comparative surveys using new (chapter 6) or archived data (chapter 3) were done to determine patterns among near-surface thermoclines and lake morphometry characteristics and phytoplankton abundance, mixing and UV-related environmental conditions. Finally, experiments (chapters 4 and 5) determined the influence of



UVR on the growth rates, elemental composition, photosynthesis, biomass and physiology of phytoplankton and bacterioplankton, under restricted mixing conditions.

## **Study Area and Lakes**

The ELA is situated in the boreal forest of northwestern Ontario in the Canadian Shield (49°40'N, 93°44'W; figure 1, Armstrong and Schindler 1971, Brunskill and Schindler 1971). Schindler et al. (1996a) reported a warming trend of 1.6°C for the ELA and surrounding region during a 20-year period (1970 -1990) and a coincident decrease in DOC concentration as a result of reduced inputs via streamflow and increased in-lake degradation (Schindler et al. 1997).

The ELA watersheds are dominated by old boreal growth forests (although some catchments have recently been burned, see chapter 3), with jack pine, black spruce, trembling aspen and white birch dominating. The trees are typically found in shallow soils on top of granite bedrock. Most ELA lakes are typically phosphorus poor (oligotrophic) with a wide range of DOC concentrations.

Lakes that were monitored are L224 (1998-99), L225 (1998), L227 (1998), L302S (1999) and L305 (1998) (Figure 1.1, Table 1.1). These lakes were chosen for differences in lake size, water clarity and physico-chemical properties. Some physico-chemical parameters are presented in Table 1.1 while other lake characteristics are presented in chapters 3 to 7 where applicable.

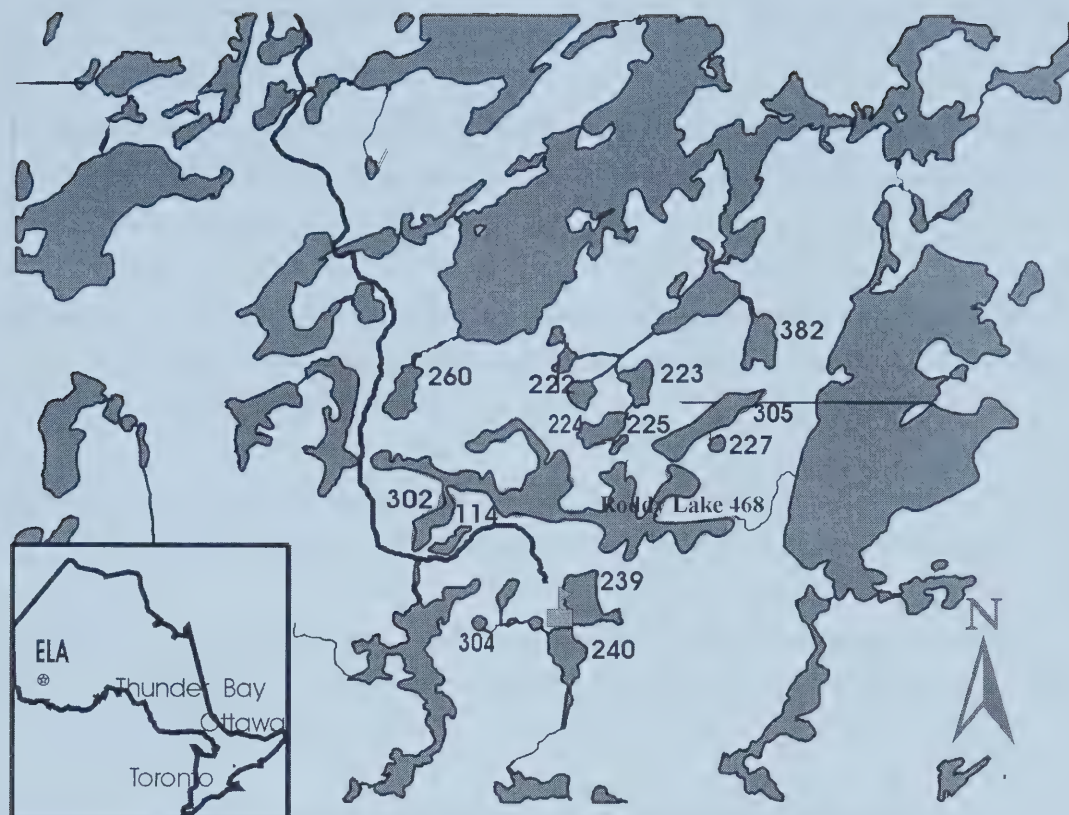


**Table 1.1.** Some physico-chemical characteristics of the lakes that were sampled.

	224	225	227	302S	305
$Z_{\max}$ (m)	27.4	4.0	10.0	10.6	32.7
$A_0$ (ha)	25.5	2.0	5.0	10.9	52.0
Thermocline (m)	6.0	1.5	3.0	5.0	7.0
$K_{dPAR}$ ( $m^{-1}$ )	0.24	1.63	1.50	0.60	0.34
DOC ( $mg\ L^{-1}$ )	3.2	9.6	11.4	4.2	3.8
1% UVB penetration (m)	1.5	0.17	0.12	0.75	1.0
Chlorophyll <i>a</i> ( $\mu g\ L^{-1}$ )	0.5-1.5	5.9-11	50-200	0.8-2.0	1.0-2.0
TP ( $\mu g\ L^{-1}$ )	4	12	20-400	8	3







**Figure 1.1.** Map of the Experimental Lakes Area (ELA) region and some of the lakes that are included in the following studies.



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## 2. PHYSICAL FACTORS DETERMINING UV FLUX INTO ECOSYSTEMS<sup>1</sup>

The shielding of the Earth from UV radiation by stratospheric ozone is but one factor in determining the exposure of organisms in the biosphere to harmful levels of UV radiation (UVR, 280-400 nm). While depletion of stratospheric ozone increases the intensity of UVB (280-315 nm), many other characteristics of the atmosphere, plant canopy, and water interact to determine the intensity of all wavelengths of UVR that reach biologically-sensitive targets. Some of these factors are also changing as the result of human-caused stressors such as climate warming and acid precipitation. All these factors are highly variable in both space and time. Here, we review some of the most important physical factors in determining the ultimate exposure of an aquatic biological target to UV.

### TRANSMISSION OF SOLAR UVR THROUGH THE ATMOSPHERE TO THE EARTH'S SURFACE

#### Introduction

Solar UVB flux through the atmosphere is a function of both atmospheric and geophysical parameters. Atmospheric transmission and radiation intensity depend on absorption by a variety of gases, of which stratospheric ozone is by far the most important, as well as scattering by air molecules, particulates and clouds. Incoming radiation is subject to absorption, re-radiation, scattering, and reflection by atmospheric constituents. The transparency of the atmosphere and clouds is a function of height and time, aerosol type and content. In addition, each atmospheric constituent has its own scattering and absorption coefficients, which vary with wavelength of solar radiation.

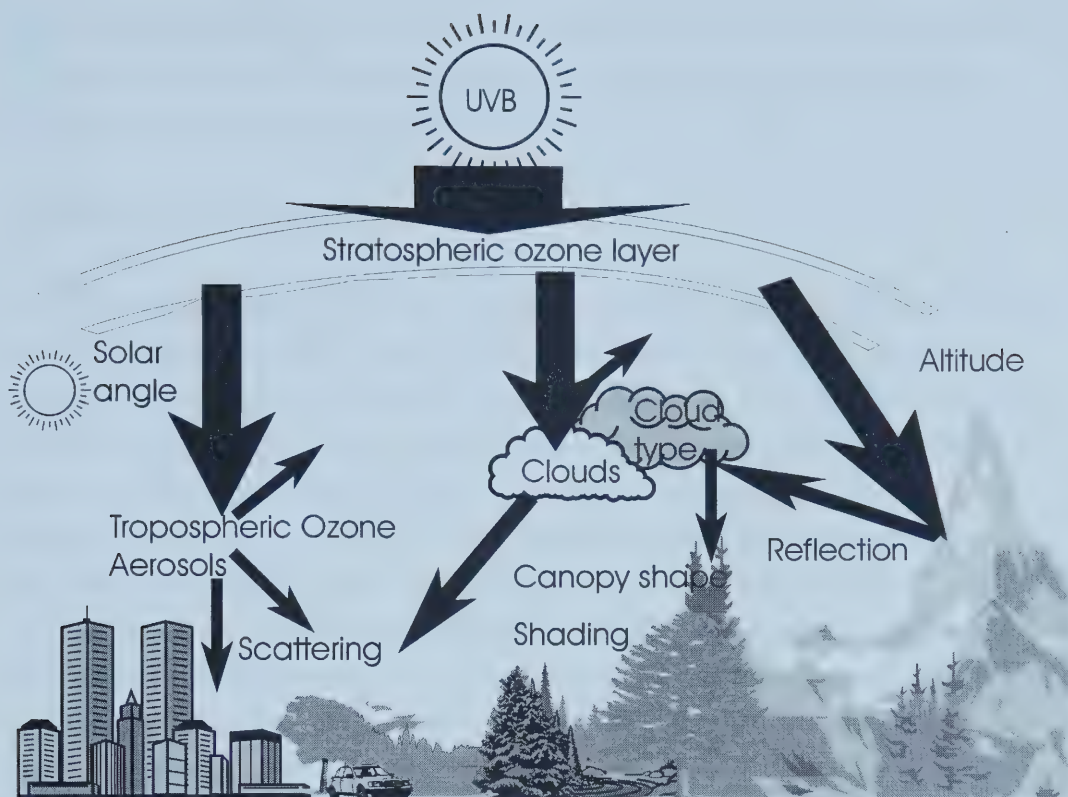
The geophysical parameters include solar elevation, latitude (hence seasonality and the Earth-sun distance), altitude and plant canopy shape (Fig. 2.1). Natural UVR intensity at the Earth's surface changes with the time of day and can vary greatly. Rapid fluctuations can occur in minutes as

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<sup>1</sup> An earlier version of this chapter has been published: M.A. Xenopoulos and D.W. Schindler. 2001. *In Ecosystems, Evolution and Ultraviolet Radiation*, pp. 36-62, C. Cockell and A. Blaustein, *Editors*, Springer Verlag, New York.







**Figure 2.1.** Summary of physical factors affecting transmission of UVB to the air/ land interface.



clouds move across the sky, and over the course of the day as the elevation of the sun changes. UVR also varies seasonally, being lower at low sun angle, although seasonal variations in stratospheric ozone concentration also have an effect.

## **Stratospheric Ozone Layer**

The stratospheric ozone layer is the gaseous protective layer found between 15 and 35 km above the Earth's surface that paradoxically is formed by an UVR-O<sub>2</sub> interaction. Increasing concentrations of trace gases such as chlorofluorocarbons (CFCs), halons and NO<sub>x</sub> are emitted by human activity. As these compounds enter the stratosphere, they lead to enhanced depletion of the ozone layer (first hypothesized by Molina and Rowland 1974; other references: Crutzen and Arnold 1986; McElroy et al. 1986; Cox and Hayman 1988). CFCs are manufactured chemicals used as coolants in refrigerators and air conditioners and as propellants in aerosol sprays. Releases of CFCs into the atmosphere have been significantly reduced since the ratification of the Montreal Protocol in 1987 (Elkins et al. 1993; Montzka et al. 1996; Environment Canada 1997). However CFCs are very stable chemicals and have life spans of 25 to 400 years; CFCs already released into the stratosphere will continue to destroy ozone for several decades (Madronich et al. 1998). Also, halons have high ozone depleting potential (10 times greater than CFCs; Environment Canada 1997) and continue to pose a threat. Halons are generally used as fire extinguishers and fire retardants.

The most notorious depletion in the ozone layer occurs at polar latitudes, especially in the Antarctic where the ozone "hole" was first discovered in 1985 by British scientists (Farman, Gardiner and Shanklin 1985). CFCs are largely released in the Northern Hemisphere and spread around the globe. However it is the extreme cold and unusual polar weather that causes the rapid Antarctic ozone depletion. Polar stratospheric clouds form during extreme cold weather (<190 K). These clouds provide a site to chemically convert chlorine and bromine particles (CFCs, halons) into reactive forms (free-radical forms). Once halogens are activated they contribute to ozone depletion through photochemical reactions (see Kumar and Häder 1999 for more details). The magnitude of this depletion is greatest around the Austral spring when the polar air is coldest and sunlight becomes important. The Antarctic ozone depletion continues to deepen; the last record low in ozone concentration (<90 DU) was established in October 2000, along with a record high in the surface area of the "hole." Recently, stratospheric ozone depletion has also been found in the Arctic (Hofmann and Deshler 1991; Manney et al. 1994; Müller et al. 1997;



Rex et al. 1997) where the small scale and uneven distribution of chemically reactant species plays a far greater role than in the Antarctic (Edouard et al. 1996). Greenhouse gases also play a role in increased stratospheric ozone losses. Although greenhouse gases warm the Earth's surface, they cool the stratosphere (through radiative cooling) accelerating ozone depletion (Shindell et al. 1998). Climate change may additionally influence Arctic ozone depletion through changes in stratospheric water vapor cycle (Kirk-Davidoff et al. 1999).

Recent data indicate that ozone depletion is not limited to polar regions. Decreases in the stratospheric ozone concentration are now measurable globally. For example, in temperate northern latitudes ozone depletion is estimated to be 4-7% per decade (Kerr and McElroy 1993; Madronich et al. 1998). Temperate southern latitudes are estimated to be losing ozone an average of 6% per decade (Madronich et al. 1998). No significant decreases in stratospheric ozone have been detected in the tropics (Madronich 1992; Niu et al. 1992), although average stratospheric ozone concentration is generally lowest near the equator.

Global measurements of stratospheric ozone concentration have been made since the late 1970s with the Total Ozone Mapping Spectrometer (TOMS) aboard various satellites. The variations in stratospheric ozone depend on the geographical location and are highly seasonal (Shoeberl et al. 1989; Stolarski et al. 1991, Stolarski et al. 1992; Krueger et al. 1992). The strongest trends are observed during the Antarctic spring (~50%, Madronich et al. 1998). In the Arctic, the largest ozone decreases occur during February and March, again following the movements of the cold polar air. From June to December, southern high-latitude regions have more negative trends than those in northern high-latitude regions. A more detailed description of seasonal and monthly trends is presented by Stolarski et al. (1992), Madronich (1992) and Niu et al. (1992). A 1% decrease in total stratospheric ozone can cause about a 2% increase in the amount of UVB radiation reaching the Earth's surface if weighted by the DNA action spectrum (see below), depending on the season and zenith angle of the sun (UNEP 1989; Herman et al. 1996).

### **Weighting Functions and Action Spectra**

Not all UV wavelengths have the same capacity to cause biological damage or stimulate photochemical reactions. The biological effectiveness of UVR increases geometrically with decreasing wavelength. This phenomenon is best described by an action spectrum or weighting function (McKinley and Diffey 1987). Action spectra describe the changing response of a given





process through the UVR region. The most widely accepted reference action spectra are those for erythema in human skin or sunburn ( $UV_{\text{erythema}}$ ; McKinley and Diffey 1987), DNA damage ( $UV_{\text{DNA}}$ ; Setlow 1974) or photoinhibition ( $UV_{\text{phot}}$ ; Jones and Kok 1966; Cullen et al. 1992). These action spectra extend throughout the 290 nm to 400 nm region but  $UV_{\text{erythema}}$  and  $UV_{\text{DNA}}$  are more sensitive to short UVR wavelengths whereas  $UV_{\text{phot}}$  is more affected at longer wavelengths. It follows that action spectra affected by UVB will be more sensitive to stratospheric ozone depletion (Madronich 1992; Roy et al. 1994). For instance, Frederick and coworkers (1998) compared total unweighted UVB,  $UV_{\text{erythema}}$  and  $UV_{\text{phot}}$  to changes in stratospheric ozone.  $UV_{\text{phot}}$  was insensitive to changes in ozone amounts, whereas the  $UV_{\text{erythema}}$  and  $UV_{\text{DNA}}$  action spectra were more sensitive to stratospheric ozone fluctuations (also shown by Roy et al. 1994). Bukata and Jerome (1997) showed that the change in the  $UV_{\text{DNA}}$  daily irradiation is considerably greater than the percentage change in daily UVB for a given change in stratospheric ozone. For an ozone depletion of 10%, the percent change in daily UVB varied from 7% to 11% while the percent in  $UV_{\text{DNA}}$  varied from 27% to 30% (Bukata and Jerome 1997).

## Clouds

Clouds play an important role in modulating UVB levels at Earth's surface because they can lead to large variations in irradiance in time and in space (McKenzie et al. 1991; Gautier et al. 1994; Lubin and Jensen 1995; Frederick 1997). Thick cloud generally reduces UVR at ground level to ~10-50% of that of clear skies (Frederick and Steele 1995; Schafer et al. 1996; Sabziparvar et al. 1999). Clouds trap solar radiation by internal scattering, so that all wavelengths take a longer effective path through a cloud. The magnitude of changes in UVR related to cloud depends on several factors such as cloud type, percent cover, water content and particle distributions within the cloud. If the cloud contains high concentrations of ozone, clouds also absorb as well as scatter radiation (see below). This will likely be the case in industrialized regions. It is interesting to note that in some cases scattering from the sides of the clouds (especially cumulus clouds) can enhance UVB (Mims and Frederick 1994; Estupiñan et al. 1996).

The ratios of UVB and UVA to PAR change within clouds and higher UVB: PAR ratios can occur under cloudy skies (Ilyas 1987; Feister 1994; Frederick 1997; Deckmyn and Impens 1998). On sunny days, in Ontario, Canada, UVB and UVA represented 0.6% and 10% of the total irradiance. However, on cloudy days, even though the absolute values were lower, UVB and UVA were higher proportions of total irradiance (1% and 16% respectively; Lean 1998).



Cloud type also plays an important role in UVR transmission (Tsay and Stamnes 1992; Lu and Khalil 1996). Tsay and Stamnes (1992) showed that low-level stratus clouds reduced UVA and UVB dose rates by ~ 60 - 75% depending on the zenith angle and ozone concentration, because strong scattering and enhanced photon path lengths inside the cloud led to both increased reflection and enhanced absorption by ozone. In contrast, higher-level cirrus clouds decreased UVB only slightly compared to clear skies under a 280 DU ozone concentration (Tsay and Stamnes 1992).

### **Absorption of UVR by tropospheric pollutants and aerosols**

Some investigators believe that increasing tropospheric pollutants such as  $O_3$ ,  $SO_2$  and aerosols (small particles suspended in air, e.g., soot, sulfate haze, dust) will decrease UVB, counteracting the trends caused by stratospheric ozone depletions (Brühl and Crutzen 1989; Bordewijk et al. 1995; Madronich et al. 1995; Varotsos et al. 1995; Zerefos et al. 1995; Ma and Guicherit 1997; Papayannis et al. 1998). Others have found that UVB may increase under a polluted troposphere. Following the El Chichon volcanic eruption, which produced an  $H_2SO_4$  aerosol layer, UVB flux in the shorter wavelengths increased relative to a clear sky (Michelangeli et al. 1992; Vogelmann et al. 1992). The increase in UVB was caused by aerosol scattering (Michelangeli et al. 1992; Tsitas and Yung 1996) especially for large solar zenith angles (Davies 1993). Also the volcanic aerosols injected into the stratosphere may induce ozone thinning by activating chlorine into forms that catalyze ozone destruction (Vogelmann et al. 1992).

While stratospheric ozone depletion has occurred since the late 1970s, tropospheric pollutants in the Northern Hemisphere have increased twofold or more over the past 100 years (WMO 1992, 1995). At mid-latitudes of the Northern Hemisphere, UVB,  $UV_{\text{erythema}}$  and  $UV_{\text{DNA}}$  at the Earth's surface may have increased by 2-5%, 4-7% and 4-10%, respectively, due to stratospheric ozone depletion since the late 1970s (Madronich 1992; Madronich et al. 1998), and decreased in the industrialized and nonurban polluted region by 5-15% ( $UV_{\text{DNA}}$ ), due to tropospheric pollution over the last 50-100 years (Liu et al. 1991; Madronich et al. 1998).

The optical properties of tropospheric aerosols vary significantly in space and time due to the size distributions, optical thickness and the different properties of the aerosols, which are wavelength dependent. For example, the single scattering albedo of aerosols may change from 0.94 in a clean



atmosphere to 0.80 in a typical nonurban polluted atmosphere (IPCC 1995). The effects of the lower tropospheric aerosols inside and over the planetary boundary layer on solar UV radiation reaching the ground are complex. Different levels of air pollution and aerosols will translate into different effects in reducing the  $UV_{\text{erythema}}$  reaching ground level (Liu et al. 1991; Varotsos et al. 1995). Solar UVR measurements in the Athens (Greece) basin revealed a substantial reduction of UVB on days with high pollution levels (Repapis et al. 1998). Summer UVB levels in Athens average more than 15% below those at other regional rural sites (Bais et al. 1996). Papayannis et al. (1998) compared two days of low and high air pollution levels but of same stratospheric ozone content, and showed a reduction of nearly 30% in the  $UV_{\text{erythema}}$  solar irradiance during local noon hours. Such a reduction, occurring during days with high amounts of pollutants like  $O_3$ , sulfurs,  $NO_2$  and aerosol particles, is both due to wavelength-dependent absorption and scattering. Brühl and Crutzen (1989) showed that tropospheric  $O_3$  absorbs UVB radiation more efficiently than stratospheric ozone. This is largely because scattering processes diffuse a large fraction of solar radiation, increasing its pathway through the atmosphere (hence longer path through tropospheric than through stratospheric ozone) and consequently increasing UVR absorption (Brühl and Crutzen 1989). The influence of sulfate aerosols and sulfur dioxide on UVB radiation has also been addressed in some studies (Zerefos et al. 1986; Bais et al. 1993; Ma and Guicherit 1997). Over 90% of the sulfate is the oxidation product of anthropogenically-emitted  $SO_2$ , which is also the primary contributor of regional acid deposition. Sulfate and  $SO_2$  also absorb strongly in the UV.

Light extinction by aerosols is highly dependent on optical thickness of the boundary layer. When a 25 km visual range was used in the calculation of total solar radiation reaching the surface, a decrease of surface solar radiation of 10% at 310 nm and 8% at 550 nm was seen for a 2 km boundary layer; for a 1 km boundary layer, this decrease was less: 7% at 310 nm and 6% at 550 nm (Liu et al. 1991).

Earth's aerosols and pollutants have the beneficial effect of reducing UVB radiation at the surface, although they have known detrimental environmental effects to health, visibility, and acid precipitation. However, aerosol effects from pollutants on UVB are expected to be negligible over remote areas. It is thus of some concern that most UVR monitoring takes place in developed countries where aerosols are more abundant. The largest UVB increases due to stratospheric ozone reduction may actually be occurring at pristine locations where they are not monitored. As a result, effects due to aerosols and other tropospheric pollutants may make UVR monitoring





results difficult to interpret for large regions. While anthropogenic sulfur, NO<sub>x</sub> and tropospheric ozone continue to increase in developing countries, North America and parts of Europe have started to decrease their emissions of SO<sub>x</sub> due to concerns for their environmental effects but not necessarily their NO<sub>x</sub> levels (Galloway et al. 1987; Hedin et al. 1994; Hedin and Likens 1996; Vitousek et al. 1997a,b).

### **Seasonality and solar zenith angle**

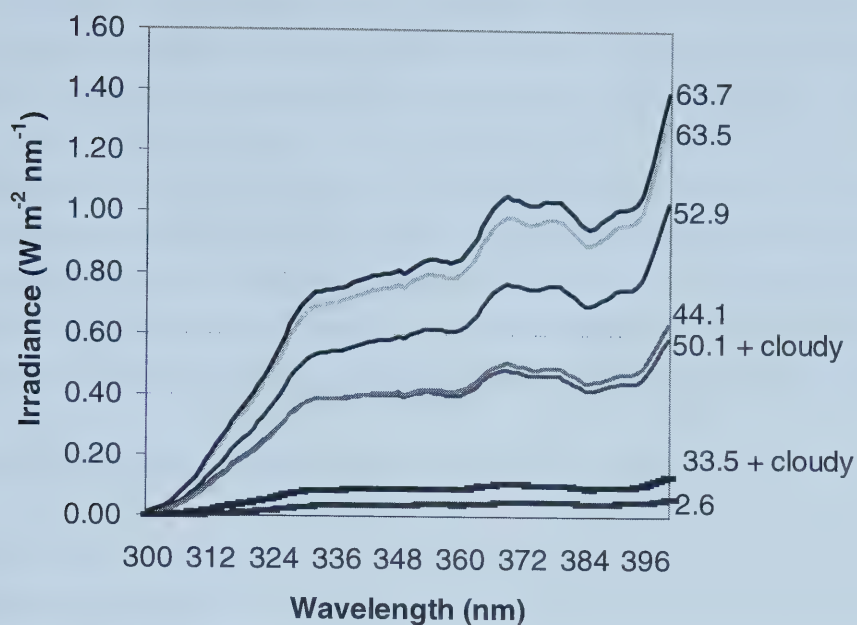
As the sun approaches the horizon, the pathlength taken by direct sunlight through the absorbing atmosphere increases, leading to a decline in UV irradiance to the ground (Fig. 2.2). The marked effect of solar altitude is apparent especially in shorter UVR wavelengths (Urbach 1997). This dependence of ground-level UV irradiance on solar elevation is related to latitude and season via the changing elevation of the sun and the duration of daylight (Frederick 1997). Annual cycles are particularly pronounced at high latitudes, where the sun fails to rise above the horizon on days near the winter solstice, and 24h per day of sunlight exists 6 months later. At temperate latitudes, accumulated radiation dose is highest in the summer season as the result of long durations of daylight and high elevations of the sun near local noon.

### **Surface albedo**

Another geophysical factor affecting UVR flux is surface albedo or reflectivity, which determines the amount of the incident radiation that is reflected from the Earth's surface back into the atmosphere. Some of this radiation can be returned towards Earth's surface increasing the incident radiation. In general, albedo is low for the UVR region and increases with increasing wavelength. Albedo values in the UVR for soil fall between 4 – 25% depending on the type of soil, surface roughness and moisture content (Feister and Grewe 1995). Values for vegetation cover average ~2% and depend on the vegetation type and age. Water reflectivity is low but depends on the angle of the sun. The albedo of ice (7-75%) and snow (20-95%) is greater but highly variable, depending on the impurities that they contain, on surface roughness and on the angle of incidence. For instance, dense dry and clean snow has a higher albedo (85- 95%) than very porous, light brown snow, soaked by water (30%). Snow albedo values can also vary with







**Figure 2.2.** UV irradiance at different wavelengths and solar angles (on the right). Data from Experimental Lakes Area (northwestern Ontario, Canada), June 16, 1998 taken using a LI-COR 1800-UW Spectroradiometer.



wavelength. Blumthaler and Ambach (1988) showed that albedo values for dry new snow were 95% for the erythema dose but only 85% for the total global radiation. As the result of greater extent and duration of snow and ice cover, high reflections generally occur in colder climates.

Surface reflections affect UV radiation both through direct reflection toward a target, and by enhancing the diffuse downwelling radiation. Beaglehole and Carter (1992) showed that in the Antarctic, the strongest skylight intensity was for light reflected from extraterrestrial direction due to simple scattering in the atmosphere induced by the high snow albedo. Madronich (1993) and Blumthaler (1993) have reviewed other measurements of surface reflectivity in the UVR range.

### **Plant canopy shape and the influences on UV exposures to the canopy**

UVR reaching plant canopies is absorbed, reflected, and transmitted by vegetation. This produces considerable variation in UV flux, in space, time and spectrum in terrestrial ecosystems. Unfortunately, measurements of UVR at the top of the canopy cannot be scaled to produce the exposure to a particular canopy or plant part (Brown et al. 1994; Parisi et al. 1996). Once the solar irradiance reaches the canopy there is leaf interception and reflection and consequent irradiance changes (Parisi et al. 1998). Several factors can influence the penetration of light through a canopy and modify the radiation environment; these are solar elevation, optical properties of plants and soils, leaf area and angles, orientation, shading by adjacent plants, inclinations, spectral albedo and the degree of reflected and transmitted radiation from foliage. In all cases, the proportion of direct and diffuse light can also greatly influence the UVB: UVA: PAR ratios and the UVB irradiance reaching the leaves at the top and the bottom of a canopy.

Taking into account plant canopy shape, a dosimetric technique was developed by Parisi and co-workers (Parisi and Wong 1994, Parisi et al. 1996, 1998) to compare ambient UVR exposure to that going through canopies. Comparison of hemispherical, conical and pinnacle shaped canopies demonstrate that UVR exposures under the canopies were reduced by 40%, 65% and 83%, respectively, compared to above the canopy (Parisi and Wong 1994). Also, for the same canopy shape, the ratio UVB: UVA changed with the sun angle. The variation throughout the day was attributed to variations in the solar zenith angle, changes in cloud cover and other transmission properties in the atmosphere.



The ratio of UVB: PAR also changes with canopy and leaf inclination (due to the higher proportion of diffuse light). Studies show that UVB penetration is less variable than PAR in a canopy (Brown et al. 1994; Deckmyn and Impens 1998). Below-canopy measurements of the UVR environment have been made under a variety of plant canopies (Lee and Downum 1991; Grant 1991; Yang et al. 1993; Brown et al. 1994; Grant et al. 1995). In low density canopies and gaps of various temperate and tropical forests, UVB is attenuated less than PAR. In contrast, PAR is attenuated less than UVB in fully leafed temperate deciduous forest canopies (Brown et al. 1994; Yang et al. 1993). Measurements under a *Sorghum* canopy of leaf area index of 7.0 showed that PAR was attenuated less than UVB when the solar zenith angle was small and more than UVB when the solar zenith angle was large (Grant et al. 1995). Grass leaves below the canopy receive light with a higher UVB: PAR ratio (Deckmyn and Impens 1998). Grant and Heisler (1996) showed that the UVB penetration into the sub-canopy of a suburban area differs greatly from that of PAR. The UVB irradiance in the shade was two-fold greater than expected. In addition, some plants are more effective in screening out UVB than others. With the use of a fiber-optic microprobe, Day et al. (1992) showed that the foliage of conifers was the most effective at attenuating UVB as opposed to leaves of herbaceous dicots that transmitted the highest amount of UVB into their mesophyll. Leaves of woody dicots and grasses were intermediate between conifers and herbaceous dicots (Day et al. 1992).

### **Altitude Effects**

Generally, solar radiation, including UVB increases with increasing altitude, because it undergoes less scattering and absorption in a thinner atmosphere. At higher altitudes the effect of tropospheric pollution on UVB radiation is also less. In addition, mountain-induced atmospheric gravity waves can cause local reductions in stratospheric temperature (Carlsaw et al. 1998) and enhance chemical reactions or chlorine activation which cause ozone destruction. This increase in solar radiation with altitude is called the altitude effect and is usually given as an increase in irradiance in per cent per 1000 m relative to sea level. The magnitude of the altitude effect under a clear-sky depends on the wavelength, sun angle, aerosols and albedo of the terrain. For instance, at low sun angle the altitude effect is stronger than at higher solar elevations (Blumthaler et al. 1997). As a result, the altitude effect is greater in winter (about 20% per 1000 m) than in summer (about 15% per 1000 m; Blumthaler et al. 1997).





The increase in UVR intensity with altitude has been measured at several sites (Blumthaler and Ambach 1990; Ambach et al. 1991; Dirmhirn et al. 1993; Blumthaler et al. 1994, 1996, 1997). A Florida weather station received less UVB than high elevation stations (Albuquerque, New Mexico; El Paso, Texas) located at similar altitudes (Scotto et al. 1988), although clouds are also more important in Florida. A comparison of daily total irradiances, between Jungfraujoch, Switzerland (3576 m above sea level) and Innsbruck, Austria (577 m a.s.l) revealed increases in irradiance with altitude of 8% per 1000 m (total irradiance), 9% per 1000m (UVA) and 18% per 1000m ( $UV_{\text{erythema}}$ ) during the summer solstice (Blumthaler et al. 1997). Measurements made in Germany showed that the altitude effect increases steadily from 9% per 1000 m (370 nm) to 11% per 1000 m (320 nm) and then more rapidly to 24% per 1000 m (300 nm) (Blumthaler et al. 1997).

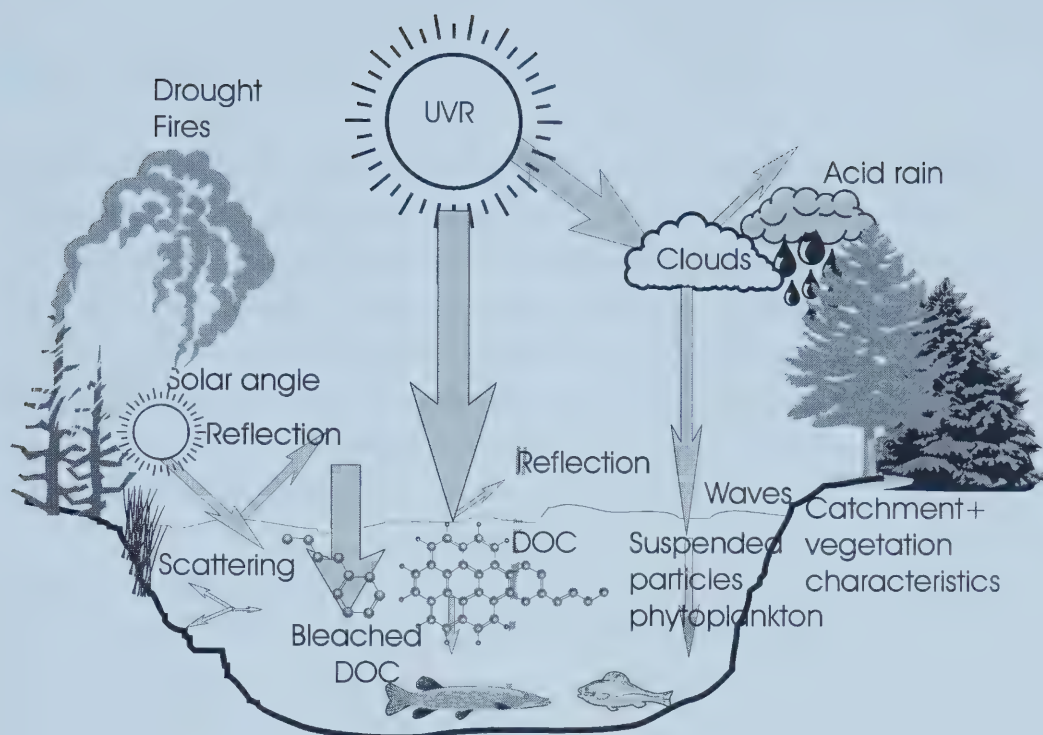
Because UVB irradiance increases with elevation above sea-level, it was suggested by a number of authors that species growing at higher altitude might be more UVB resistant. Some investigators have found that plant species and populations originating from naturally high UVB (high altitudes) are less sensitive to increased levels of UVB than species found in low UVB locations (e.g. Caldwell et al. 1982; Larson et al. 1990; Sullivan et al. 1992; Somersalo et al. 1998). However, others have found little change in sensitivity with increasing UVB exposure (van de Staaij et al. 1995; Rau and Hofmann 1996).

## TRANSMISSION OF SOLAR UVR THROUGH WATER

### Introduction

The irradiance at a given depth and wavelength in lakes and oceans depends on a number of parameters including the angle and intensity of surface irradiance and the properties of the water column (Fig. 2.3; Hutchinson 1957; Kirk 1994a, b). The depth of the water required to remove 99% of the solar radiation at 310 nm varies from about 30 m in the clearest and most colorless ocean water to a few centimeters in brown humic lakes and rivers. In this section we will consider the factors that affect UVR penetration in waters.





**Figure 2.3.** Summary of factors affecting transmission of UVR to the air/ water interface and through the water. See text for details.



## UVR distribution in the water

The transmission of UVR through the air-water interface varies with time, due to changes in the distribution of UVR and to the effect of surface waves (Stramski et al. 1992), which both modulate intensity at a particular depth, and the amount reflected back into the air. Water reflectivity is inversely related to solar angle and ranges from 5% when the solar zenith angle is greater than  $30^\circ$  to more than 60% when the solar altitude is less than  $3^\circ$  degrees. Loss by reflection is lowest ( $\sim 2 - 3\%$ ) during midday when the angle of the sun is high (Kirk 1994b). Additionally, rough seas have a somewhat lower albedo than calm seas, although the difference is small (Jerome and Bukata 1998).

The radiance distribution below the water surface is subject to absorption and scattering by dissolved and particulate matter, the magnitude of which is wavelength-dependent. Pure freshwater or seawater has a high transmission in the UVR ( $> 87\%$  of surface irradiance at 300 nm, Smith and Baker 1981). Most of the UVB photons in natural waters are absorbed by dissolved (gelbstoff or gilvin) and particulate organic substances, present in all natural waters, and originating mainly from the breakdown of terrestrial plant biomass in the soils of the catchments from which the waters are derived.

The concentrations of dissolved organic carbon (DOC) compounds and suspended particles primarily influence UVR transmission, leading to large differences in UVR transparency among water bodies. In the euphotic zone, UVB radiation is much more rapidly attenuated than PAR. Similarly  $UV_{DNA}$  is attenuated more rapidly than unweighted UVB (Jerome and Bukata 1998). With the exception of some high-altitude alpine lakes or high latitude polar lakes, inland waters, because of their higher humic content, attenuate UVB more intensely than marine waters. However, marine waters can also show large differences in their optical properties in UVR. The concentrations of dissolved absorbing substances undergo a drastic change from oceanic to coastal water types. Jerlov (1950) found that UVB (310 nm) was reduced by only  $14\% m^{-1}$  in the middle of the Mediterranean Sea but this reduction increases to over  $90\% m^{-1}$  in a more coastal area. This difference in UVR attenuation between oceanic and coastal stations has also been observed off the central Chilean coast (Montecino and Pizarro 1995) and in the Baltic Sea (Piazena and Häder 1997). Jerlov (1968) further classified marine waters into several types of coastal and oceanic waters depending on their transmission (but see Piazena and Häder 1997).



## Optical properties of natural water and UVR absorbing substances

The absorption of light by a given molecule occurs when the molecule's electrons resonate at frequencies that correspond to a photon's energy state. DOC contains chemical structures or chromophores that highly absorb UVR and is by far the most important absorber of UVR. The most common DOC classes are fulvic acids, tannic acids and lignins; compounds which are composed of aromatic groups and aliphatic chains in different proportions. The aromatic group absorbs more light than the aliphatic portion of the DOC.

One of the biggest difficulties today is attempting to chemically classify DOC because there are differences in absorption coefficients, chemical and optical characteristics of DOC from one site to the next (Bricaud et al. 1981; Malcolm 1990; McKnight et al. 1991, 1994; Jerome and Bukata 1998). A large range of variation is reported in aquatic environments (Malcolm 1990; McKnight et al. 1991, 1994), further complicating comparisons between sites.

DOC sources are generally qualified as either allochthonous (terrestrially-derived) or autochthonous (derived from in-lake metabolism) and have very different optical properties. Allochthonous DOC is colored, high molecular weight and contains a high proportion of aromatic residues. It is derived from vegetation and terrestrial soils and is composed of differing proportions of aromatic humic and fulvic acids. Autochthonous DOC is microbially derived, usually from algal-rich environments. This type of DOC has higher nitrogen content and less aromaticity than terrestrially-derived material

Specific absorbance is but one optical property of DOC. DOC is very highly absorptive in the UVR (Scully and Lean 1994; Morris et al. 1995). DOC absorbance can vary greatly between sites. For example, DOC in prairie saline lakes (or closed basin lakes) is more "transparent" than DOC from boreal forest lakes (Curtis and Schindler 1997; Jerome and Bukata 1998). Photobleaching is the interaction of DOC and light resulting in the loss of conjugated double bonds (aromaticity) and photolysis of larger molecules (Wetzel et al. 1995), increasing UVR penetration. Photobleached DOC contains far less aromatic structures than DOC from a boreal system. Closed basin lakes have longer water renewal times (100 years or more) resulting in decades or even centuries of photobleaching (Curtis and Adams 1995). Fluorescence, another optical property of DOC, is useful for distinguishing between bleached allochthonous and autochthonous DOC (Donahue et al.





1998) as its intensity is lower for autochthonous DOC. It is interesting to note that photolysis of DOC yields biologically available products (e.g. glyxolate and pyruvate) that are readily taken up by bacterioplankton thus enhancing microbial activity (Wetzel et al. 1995; Herndl 1997). In spite of that, the photochemical breakdown of DOC exceeds the microbial degradation of DOC by several orders of magnitude (Molot and Dillon 1997).

Catchment characteristics are important in determining DOC type and concentrations. Lakes and streams at high altitudes and latitudes generally have catchments with little vegetation, and soils containing little organic material (Schindler and Curtis 1997; McKnight et al. 1997). Similarly DOC from polar desert catchments have a reduced ratio of aromatic to aliphatic organic residue (McKnight et al. 1994). Typically, wetlands have the highest DOC concentration (10-50 mg C L<sup>-1</sup>; Curtis 1998) and alpine lakes the lowest (0.05-3.0 mg C L<sup>-1</sup>; Baron et al. 1991). Rates of export of DOC are high in peatlands and bogs, having a profound impact on lake color (Urban et al. 1989). Furthermore, DOC from bogs contain a greater fraction of aromatic fulvic acids (McKnight et al. 1985). In general, there is a positive relationship between the relative drainage area (catchment area: lake surface area) and DOC inputs (Rasmussen et al. 1989; Curtis and Schindler 1997; Curtis 1998), while water color (and DOC content) is inversely proportional to water residence time (Curtis and Schindler 1997; Dillon and Molot 1997).

Climate also interacts with topography and geology to modify DOC loadings in aquatic systems (Curtis 1998). This invariably causes high interannual variability in DOC inputs resulting from differences in precipitation, streamflow and residence in lakes (Schindler and Curtis 1997; Schindler et al. 1997). Typically DOC content declines from spring to fall (Hessen et al. 1997). However, a single storm event can increase DOC inputs by as much as ~ 400% in streams (Hinton et al. 1997).

Very little information exists on absorption and scattering of UVR by phytoplankton, other particulates or suspended minerals or sediments. Particulate material is important in attenuation of UV in marine systems and in the Laurentian Great Lakes where there is little attenuation by dissolved substances (Kirk 1994a; Smith et al. 1999) but not in smaller lakes where the correlation with chlorophyll is rather weak (Scully and Lean 1994) and most attenuation of all solar wavelengths is by colored organic matter (Schindler 1971). However, it is known that certain algae, macroalgae and cyanobacteria can synthesize a variety of compounds that strongly absorb in the UVR. Such compounds are scytonemin (Garcia-Pichel and Castenholz 1991) and



mycosporine-like amino acids (Garcia-Pichel and Castenholz 1993). These compounds are also found in consumers that take them up with their food.

The fraction of photons absorbed by chlorophyll and DOC is wavelength dependent. As shown by Jerome and Bukata's (1998) photon budget for inland waters, only 5% of UVA and UVB photons are reflected by the air-water interface or absorbed by pure water. The remaining 90% are absorbed by DOC (55% – 86%) and phytoplankton (5% – 35%), depending on the wavelength. Chlorophyll absorbs only a small fraction (~5%) of UVB photons but displays two absorption peaks at 338 nm (25%) and 400 nm (35%) at which wavelengths DOC displays minima in absorption.

### Vertical attenuation coefficients and measurements

Vertical attenuation coefficients ( $K_d$ ) for solar radiation are calculated from the slope of the regression of the rate of decrease in UVR penetration with depth below the zone where surface reflectance affects measurements. Coefficients range from  $0.05 \text{ m}^{-1}$  in the clearest waters to  $>30 \text{ m}^{-1}$  in dark brown, humic waters. These translate in UVR penetration depths from several dozen meters in the clearest ocean waters (Gieskes and Kray 1990; Smith et al. 1992; Booth and Morrow 1997) to a few centimeters in humic lakes (Lean 1998).

Empirical models that predict the  $K_d$  have been devised by Smith and Baker (1981) to allow prediction of attenuation and irradiance penetration from water column content of DOC and suspended constituents (chlorophyll). Scully and Lean (1994) described the relationship of the attenuation of UV in lakes between chlorophyll, dissolved organic carbon (DOC) and particulate organic carbon (POC) and found that attenuation coefficients of UVB and UVA could be predicted using empirically derived equations.  $K_d$  (UVB and UVA) correlated best with DOC and was found to be a power function of the concentration of DOC (Scully and Lean 1994):

$$1) \quad K_{d\text{UVB}} = 0.415 (\text{DOC})^{1.86}; r^2 = 0.97$$

$$2) \quad K_{d\text{UVA}} = 0.299 (\text{DOC})^{1.53}; r^2 = 0.95$$

Schindler et al. (1996b), refitted the data to predict the maximum (1% surface) depth of UVB penetration, using a slightly more complex equation:

$$1\% \text{ UVB} = 5.173 (\text{DOC})^{-0.706} - 1.029; r^2 = 0.98.$$



These empirical relationships are poor for lakes with DOC concentrations  $> 8 \text{ mg C L}^{-1}$  (Lean 1998) or for closed basin lakes where DOC is highly photobleached, but serve as a useful approximation of optical properties in the UVR range for most lakes.

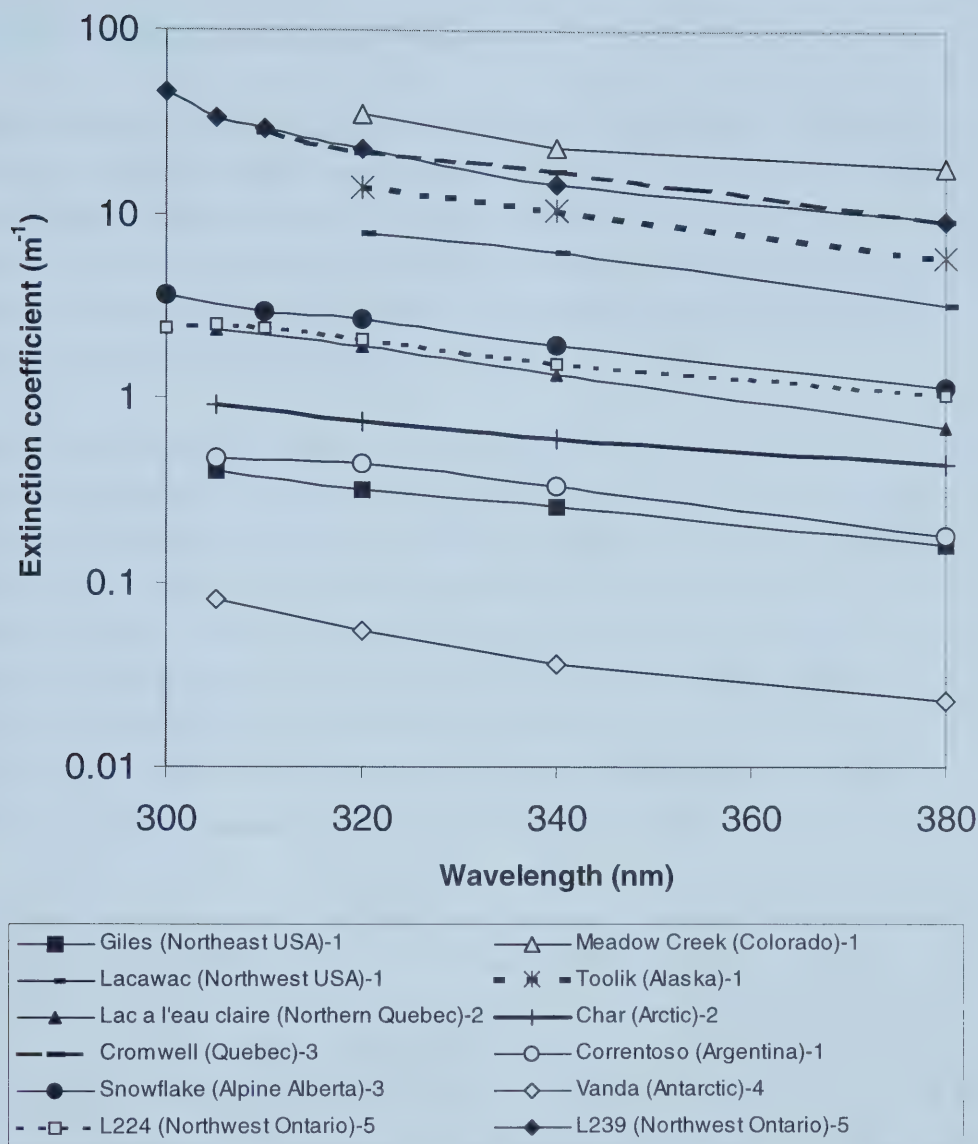
Freshwater lakes show tremendous variability with respect to penetration and attenuation of UVR; almost 1000-fold (Fig. 2.4). Concentrations of DOC range from  $<1 \text{ mg C L}^{-1}$  in transparent lakes (mainly alpine or polar lakes) to  $50 \text{ mg C L}^{-1}$  in bog waters. Of the 16 Canadian and alpine lakes from the Scully and Lean (1994) study, all but one lake exhibited  $K_d$  values in the UVB greater than  $1.0 \text{ m}^{-1}$ . Morris et al. (1995) conducted a similar study with 59 lakes from northeastern U.S., Colorado, Alaska and Argentina for which DOC concentrations were between 0.2 and  $23 \text{ mg C L}^{-1}$  and  $K_{d305}$  between  $\sim 0.2 \text{ m}^{-1}$  and  $130 \text{ m}^{-1}$ . The lowest  $K_d$  value ( $0.2 \text{ m}^{-1}$ ) was for an alpine lake in the high Andes and the highest were in high DOC humic lakes. Similarly, high-latitude lakes from the Canadian high Arctic and subarctic Quebec exhibited  $K_{d305}$  values between  $<1 \text{ m}^{-1}$  and  $\sim 40 \text{ m}^{-1}$  (Laurion et al. 1997).

Even a few centimeters of snow cover would effectively block UV from entering lakes and oceans, as it does for PAR (Schindler and Nighswander 1970). However, in the absence of snow, ice is highly transparent to UV in lakes (Vincent et al. 1998) and oceans (Trodahl and Buckley 1990). In a comparison of four Antarctic permanently ice-covered lakes, Vincent et al. (1998) found that UVR penetrated well beneath the ice in all four lakes. Because their polar desert catchments are devoid of any vegetation, these lakes receive very small amounts of allochthonous DOC. Attenuation coefficients for Lake Vanda, an ultraoligotrophic Antarctic lake were the lowest published (Fig. 2.4). UVB (305 nm) penetrated past 30 m and UVA (380 nm) at 60 m.

Declines in DOC levels resulting from climatic warming and acid precipitation (see below) can dramatically increase penetration of UVB and PAR. Below a threshold of  $\sim 2\text{-}3 \text{ mg DOC L}^{-1}$ , UVR penetration increases rapidly (Morris et al. 1995; Schindler et al. 1996; Williamson et al. 1996; Laurion et al. 1997). These low DOC levels are typical in about a third of the lakes in North America's boreal forest but in a higher proportion of alpine and arctic lakes. High UVR exposure from low DOC levels could stimulate pigment formation in zooplankton (Byron 1982; Hessen 1993; Vinebrooke and Leavitt 1999) and algae (Leavitt et al. 1997) in alpine lakes.







**Figure 2.4.** Attenuation coefficients for various lakes differing in DOC concentration. Data from (1) Morris et al. 1995; (2) Laurion, Vincent and Lean 1997; (3) Scully and Lean 1994; (4) Vincent et al. 1998; (5) S.J. Page, Freshwater Institute, Winnipeg, Canada, unpublished data.



## **Vertical stratification, mixing and flowing waters**

Shallow depths and seasonal stratification can potentially expose plankton and benthos to harsh UVR environments. In shallow clear alpine lakes and ponds, high UVR can penetrate the entire water column. Seasonal stratification is also likely to affect exposure in lakes especially when near-surface shallow stratification occur in lakes (Milot-Roy and Vincent 1994; Xenopoulos et al. 2000). Near-surface thermoclines are frequent in boreal lakes, particularly in small lakes (Xenopoulos and Schindler, in press, see chapter 3).

Meteorological conditions can influence the variability of underwater irradiance. Under sunny skies and slightly windy conditions, PAR and UVR values were more variable than during sunny and windless conditions (Laurion et al. 1997). This variation was spectrally dependent, PAR values at 30 cm depth varied by ~20% whereas UVR varied only by 5% (Laurion et al. 1997). Piazena and Häder (1994) noted some noise in their irradiance curves when waves and clouds were present. They also showed that both total mixing and strong surface stratification can influence the UV fluence rates in coastal lagoons. During strong mixing and negligible stratification of temperature and salinity in the water column, the vertical gradients of transmission differed only little from a linear slope on a semilogarithmic scale.

DOC is also probably the most important factor determining the amount of UVR exposure in streams and rivers. The larger fraction of DOC in streams is the refractory allochthonous DOC (McDowell and Fisher 1976). However, shading by the forest riparian canopy is potentially another important factor affecting UVR exposure in flowing waters. Removing an entire canopy increased the UVB reaching streams by 500% (Kelly 2001). This increase in UVB can lead to dramatic reorganization of invertebrate and algal communities (Bothwell et al. 1994; Donahue and Schindler 1998).

## **Synergistic interactions of UVR and climate change**

Because of the negative exponential relationship between DOC and UVR, lakes with  $< 2\text{--}3 \text{ mg C L}^{-1}$  allow high exposure of aquatic communities to UVR. There are now records of declining levels of DOC following climate warming (Schindler 1997; Schindler et al. 1996a, b, 1997). Schindler et al. (1996a) reported a warming trend of  $1.6^{\circ}\text{C}$  for the boreal forest of northwestern



Ontario during a 20 year period (1970 -1990) and a coincident decrease in DOC concentration as a result of reduced inputs via streamflow and increased in-lake degradation (Schindler et al. 1997). In particular, precipitation decreased by 25%, evaporation increased, and forest fires increased. Forest fires cause decreased DOC inputs by increasing mineralization of soils (Schindler et al. 1997). Also, water renewal times of lakes were increased, enhancing photobleaching and mineralization of DOC to carbon dioxide (Dillon and Molot 1997). Overall climatic warming caused DOC to decline 15-25% (Schindler et al. 1996b, 1997) and increased UV penetration by 30% in boreal lakes. Such patterns are expected to be magnified in alpine, arctic or acidified lakes where low DOC content provides less protection to the biota.

### **Synergistic interactions of UVR and acid rain**

Acidified lakes are known to lose DOC (Davis et al. 1985; Effler et al. 1985; Schindler et al. 1996b, 1997; Yan et al. 1996). Both precipitation and mineralization of DOC are increased (Dillon and Molot 1997; Schindler et al. 1997). DOC declined 80% in an experimentally acidified lake of the Experimental Lakes Area (Ontario, Canada, Schindler et al. 1997; Schindler 1998), increasing UVR penetration by nearly 900% (Donahue et al. 1998). Humic acids are coagulated and precipitated into the sediments following protonation from acidity. However acidification does not only affect the quantity of DOC it also changes its optical properties significantly reducing its capacity to absorb light (Donahue et al. 1998). It was hypothesized that the decrease in pH, increased the oxidation of humic DOC leaving only the aliphatic portion of the aromatic ring (Donahue et al. 1998).

### **Conclusion**

UVB represents less than 1% of the total solar flux reaching the Earth's surface. However, it is highly energetic and its impact on organisms can be substantial, from damaging macromolecular cellular structures up to possible alterations in primary productivity, structure and function of ecosystems. Consequently, it is essential to understand and have accurate characterization of UVB transmitting through the atmosphere and reaching the Earth's boundary layer and aquatic ecosystems. Physical factors in atmosphere and water affect the UV exposure of organisms in a complex manner. When determining UVR exposure one cannot take into account stratospheric ozone concentration alone. Air pollution, clouds, plant canopy and albedo can all interact with stratospheric ozone depletion and influence UVR exposure on ecosystems. In aquatic systems a



range of factors interact to determine UVR exposure, such as basin size and dissolved organic substances. Gorham (1996) referred to the complex interaction of a depleting stratospheric ozone, climate warming and acidification as the “three-pronged attack”. All three are anthropogenic-induced stressors and contribute together in exacerbating the effects of increased UVR exposure of aquatic systems.





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### 3. ENVIRONMENTAL CONTROL OF NEAR-SURFACE THERMOCLINES IN BOREAL LAKES<sup>2</sup>

#### INTRODUCTION

Thermal stratification influences biological, chemical and physical processes in lakes, including nutrient cycling, primary production, depth distribution of organisms and water movement (Schindler et al. 1996a, Sellers et al. 1998). Seasonal thermocline depth is influenced by lake size and water clarity (Gorham and Boyce 1989; Mazumder et al. 1990; Fee et al. 1996). As lake area increases, wind fetch increases and seasonal thermoclines deepen (Arai 1981; Patalas 1984; Fee et al. 1996; King et al. 1997). Recent studies have shown that changing climatic conditions (Schindler et al. 1990, 1996a, b; King et al. 1999; Snucins and Gunn 2000) and logging (Scully et al. 2000; Steedman and Kushneriuk 2000) can also influence thermocline depths in lake ecosystems.

In addition to a main seasonal thermocline, near-surface thermoclines (also called secondary thermoclines, transient thermoclines or diurnal thermoclines) form under sunny and near windless conditions (Imberger 1985) and can retain the plankton under photoinhibitory irradiances (Vincent et al. 1984). Near-surface thermoclines can be as shallow as 0.3-1m. They can isolate the upper part of the epilimnion for periods of several hours during daylight, but are usually destroyed by convective mixing at night (Imberger 1985; Imberger and Patterson 1990). Any organisms trapped in the near-surface layer can be exposed to high solar irradiances, including UVB radiation, with attendant effects on their growth and physiological state (Vincent et al. 1984; Milot-Roy and Vincent 1994; Xenopoulos et al. 2000; Xenopoulos et al. in press). Near-surface thermoclines can influence phytoplankton production and species composition (Lewis et al. 1984; Vincent 1990; Frenette et al. 1996; Berman and Shteinman 1998; Sherman et al. 1998). Phytoplankton in different layers can also have different photoadaptive properties (Falkowski 1983; Lewis et al. 1984). Despite their recognized importance to biological processes, no study has examined the frequency of occurrence of transient, near-surface thermoclines. The presence of near-surface thermoclines usually goes unnoticed although they may have subsequent effects

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on many biological (e.g. UV damage of phytoplankton, Xenopoulos et al. 2000) or chemical processes (e.g. diurnal photobleaching of dissolved organic matter, Gibson et al. 2001).

We hypothesized that like seasonal thermoclines, the formation of near-surface thermoclines would be affected by lake size, water transparency, temperature, and wind. We based our analysis on approximately 25 years of data from nearly 40 lakes spanning several orders of magnitude in size and a wide range of water transparency. We show that near-surface thermoclines are unexpectedly common even in large lakes.

## METHODS

### Study site

All lakes used in this study are located in the Canadian Shield in northwestern Ontario's boreal forest. They therefore experience similar climate and are surrounded by similar topography and vegetation. Twenty-five years of archived temperature data from the Experimental Lakes Area (ELA; 49°40'N, 93°44'W) were used initially to detect size-related differences in the frequency of occurrence of near-surface thermoclines (Table 3.1).

Over the period of study, ELA experienced climatic warming, with progressively warmer and drier weather during the 1970s and 1980s, resulting in severe forest fires around the ELA watersheds that may have contributed to an increase in wind velocity (Schindler et al. 1990, 1996a; France 1997). Forest fires play a major role in determining the distribution of terrestrial plants and animals of this region. It appears that the ELA region is subjected to forest fires on average every 50 to 100 years.

To examine the frequency of near-surface thermoclines in larger lakes, we used data from the Northwest Ontario Lake Size Series (NOLSS) study, and lakes Superior and Nipigon (Table 3.1; Fee and Hecky 1992; Fee et al. 1992). The NOLSS lakes are located in the Red Lake District of northwestern Ontario (51°N, 94°W, 150 km north of ELA). Morphometric details of the lakes and the NOLSS study are presented in Fee and Hecky (1992) and Fee et al. (1992). A summary of the ELA and NOLSS data is shown in Table 3.1.



**Table 3.1.** Surface area ( $A_0$ ) maximum depth ( $z_{\max}$ ), average light attenuation ( $K_d$ ) and standard deviation of data used, number of temperature profiles used in analysis, sampling years for which temperature profiles were available and current watershed status for each of the ELA and NOLSS lakes used in this study.

Lake	$A_0$ (ha)	$z_{\max}$ (m)	$K_d$ ( $m^{-1}$ )	# temp. profiles	Sampling years	Current watershed status
93	5.3	8.2	$0.74 \pm 0.09$	16	84, 85	Forested
103	2.3	4.2	$1.73 \pm 0.26$	9	74, 75	Forested
109	15.5	10.1	$0.40 \pm 0.08$	89	83-93	Forested
110	5.3	12.8	$0.50 \pm 0.07$	43	83-88	Forested
111	9.3	32.0	$0.49 \pm 0.05$	12	87-90	Forested
114	12.1	5.0	$0.68 \pm 0.17$	101	69, 71, 74, 78, 79-86, 88, 89	Logged (1973)
120	9.3	19.0	$0.62 \pm 0.08$	16	69, 71, 72, 74	Forested
221	9.0	5.7	$1.11 \pm 0.24$	56	85-90	Forested
222	16.4	5.8	$1.15 \pm 0.25$	98	80-92	Forested
223	27.3	14.4	$0.37 \pm 0.10$	189	74-94	Forested
224	25.9	27.4	$0.24 \pm 0.04$	163	74-78, 81-94	Forested
225	4.0	2.0	$1.63 \pm 0.36$	23	87-89	Forested
226	16.1	14.7	$0.69 \pm 0.19$	364	71, 73-82, 84-94	Part. Burned (1979)
227	5.0	9.0	$1.50 \pm 0.53$	265	68-94	Forested
230	1.7	13.6	$0.93 \pm 0.16$	21	68-72, 75, 76	Burned (1974)
239	56.1	30.4	$0.65 \pm 0.14$	257	69-94	Burned (1974, 1980)
240	44.1	13.1	$0.60 \pm 0.14$	197	69-72, 74-78, 80-94	Burned (1974, 1980)
260	34.0	14.4	$0.54 \pm 0.05$	28	86-90	Part. Logged (1973-1981), Part. Burned (1979)
261	5.6	9.6	$1.04 \pm 0.18$	65	70-78	Forested
302	23.7	13.8	$0.54 \pm 0.13$	342	72-78, 80-94	Forested
303	9.5	2.5	$1.03 \pm 0.37$	55	69-71, 74-78	Burned (1980)
304	3.4	6.7	$1.15 \pm 0.30$	106	60-77, 85-86	Burned (1980)
305	52.0	32.7	$0.35 \pm 0.05$	84	68, 69, 71, 72, 74, 85-94	Forested
373	28.0	21.5	$0.30 \pm 0.05$	101	83-94	Part. Logged (1978)
374	485	30.0	$0.33 \pm 0.05$	44	83-89	Part. Logged (1970s)



Table 3.1 continued

375	18.9	26.5	0.42 ± 0.05	38	83, 86-90	Part. Logged (1978)
382	37.1	13.1	0.66 ± 0.09	114	77-80, 83-94	Forested
383	5.6	9.7	0.83 ± 0.13	8	74, 75	Burned (1974)
622	37.0	30.5	0.51 ± 0.06	7	83	Part. Logged (1970s)
623	36.0	21.3	0.46 ± 0.05	23	83-85	Part. Logged (1970s)
629	62.5	18.0	0.52 ± 0.07	24	83-85	Forested
Green	89.0	19	0.48 ± 0.06	66	86-95 (excluding 92)	Forested
Linge	706	23	0.65 ± 0.08	60	86-95 (excluding 92)	Forested
Musclow	2 220	46	0.64 ± 0.07	48	86-95 (excluding 92)	Forested
Nipigon	484 800	143	0.48 ± 0.10	51	89-91	Forested
Orange	167	29	0.62 ± 0.07	61	86-95 (excluding 92)	Forested
Superior	8 223 600	403	0.18 ± 0.02	11	90, 91	Largely undevelopped
Sydney	5 750	73	0.50 ± 0.05	46	86-95 (excluding 92)	Forested
Trout	34 700	49	0.38 ± 0.06	43	86-95 (excluding 92)	Forested



## Temperature measurements

Temperature profiles of the ELA lakes have been measured on a regular basis since 1968. Temperature measurements were usually taken during the morning collection of lake water chemistry samples, generally between 8AM and noon (Cruikshank 1984, 1988, 1994). Temperature profiles of the ELA lakes were taken weekly or twice monthly for most of the lakes. In the earlier years (1968-1980) ELA temperature measurements were taken using a Whitney thermistor with an accuracy of  $0.1^{\circ}\text{C}$ . All other ELA temperature profiles were taken using a Flett Research Mark II Digital Telethermometer (accuracy  $0.1^{\circ}\text{C}$ ). All thermistors were calibrated frequently with a National Bureau of Standards mercury thermometer with an accuracy of  $0.02^{\circ}\text{C}$ . Profiles were obtained by starting at the lake surface and taking temperature (T) readings at one meter intervals. Near-surface thermoclines were then judged to be present when  $T_{0\text{m}} - T_{1\text{m}}$  was  $\geq 0.2^{\circ}\text{C}$ . Only the period of summer stratification was considered (when surface  $T > 8^{\circ}\text{C}$ ). By inspection, we also eliminated the rare cases where the depth of the main thermocline was  $< 1.1\text{ m}$  in our temperature profiles.

In 1986 and 1987 temperature measurements from the NOLSS study were made using the Flett thermistor as above. After 1987, temperature measurements were made with a free-falling temperature profiler (R. Brancker, Ltd, Ottawa, Ont., accuracy  $0.05^{\circ}\text{C}$ ) that measured temperature at depth intervals of  $\sim 0.05\text{m}$ . For analytical consistency, the same criterion for the presence of near-surface thermoclines was applied as for the ELA data. Although a temperature difference of only  $0.02^{\circ}\text{C}$  is sufficient for near-surface thermoclines to develop (e.g. Imberger 1985), we decided to use a temperature difference of  $0.2^{\circ}\text{C}$  to describe near-surface thermoclines in this study, given the accuracy of our thermistors ( $0.05^{\circ}\text{C}$  and  $0.1^{\circ}\text{C}$ ). We also chose to consider only the summer stratification (mid-May to mid-September) period (when surface  $T > 8^{\circ}\text{C}$ ), which is the period of highest biological activity. During this period the surface temperature is high enough so that the density difference established between the surface and 1 m generally lasts well into the day. In total 3344 profiles from 39 ELA and NOLSS lakes were used.

The instruments were cross-calibrated to correct for the difference in thermistor sensitivity (accuracy). Temperature profiles were taken simultaneously with both Flett and Brancker thermistors on several occasions during the summer of 1998 in three ELA lakes. A calibration factor was calculated and applied to the ELA dataset to facilitate comparisons.





## Wind measurements

Daily wind velocities were measured with an Atmospheric Environment Service (AES) anemometer and anemograph, type 45B, located at the ELA meteorological site, approximately 350 m west of the shores of Lake 239 (one of the reference lakes at the ELA). Additional details on wind measurements are presented in Beaty (1981, 1984) and Beaty and Lyng (1989). Wind velocities were measured hourly from 1969-1994, 10 m above ground. The wind data reported here are means of the hourly measurements for the ice-free season of each year. Wind at the surface of the lake (field wind data) is available for ELA only after 1990. It was measured at the center of the ELA lakes with a hand-held anemometer (Davis Instruments, Turbo-meter) at the same time as the temperature profile (instantaneous measurements at approximately 1 m height). Wind measurements at the surface of the NOLSS lakes are not available.

## Water density calculations

The Brünt-Väisälä ( $N$ ) frequency was calculated as a thermal stability index as in Spiegel and Imberger (1987):  $N = (g/\rho_o \cdot d\rho/dz)^{1/2}$ , where  $g$  is the acceleration due to gravity,  $\rho_o$  is the maximum density in the water column and  $d\rho/dz$  is the vertical density gradient (for 0m – 1m). Density profiles were calculated for ELA only from temperature measurements when  $T_{0m} \geq T_{1m}$  and  $T_{0m} > 8^\circ\text{C}$ .

## Extinction coefficient

For ELA and NOLSS, extinction coefficients ( $K_d$ ) of photosynthetically active radiation (PAR) were calculated from the statistical regression of the natural logarithm of light on depth (Fee et al. 1991). All  $K_d$  values were averaged for each lake for the whole available sampling period.

## Statistical analysis

The environmental variables (surface area, wind and  $K_d$ ) were tested using linear or where applicable, non-linear regressions for their ability to explain the variance in the frequency of near-surface thermoclines. Only the best fitting models (as determined from  $r^2$  comparisons) are presented here. The critical probability level was adjusted using the Bonferroni approach to  $\alpha =$



0.0025, for the relationship between surface area and near-surface thermoclines for which several non-linear regressions and transformations were tested. Inter-correlation amongst independent variables negated the possibility of using multiple regression analysis in this study. All regressions were done using JMP (SAS Institute 1996).

## RESULTS AND DISCUSSION

### The influence of lake size

Near-surface thermoclines occurred on a high proportion of summer days in all lakes, except for Lake Superior. The incidence decreased with increasing lake size (surface area,  $A_0$ ; Fig. 3.1). At the ELA, near-surface thermoclines generally occurred on over 40% of all summer days in lakes under 50 ha in surface area. In smaller lakes (~2 ha) the frequency increased to ~90% (Fig. 3.1). The much larger NOLSS lakes also showed a high frequency of near-surface thermoclines, ranging from 25% (Nipigon) to ~40% (Musclow, Sydney and Trout). Near-surface thermoclines, as defined here, were not detected in Lake Superior. The frequency of near-surface thermoclines in boreal lakes declines rapidly with lake area from 2 to 100 ha, then reaches an asymptote for larger lakes where near-surface thermoclines occur about one-third of the time during the summer.

While our analysis indicates a strong relationship between occurrence of near-surface thermoclines and lake size, it probably underestimates the actual frequency of occurrence. Near-surface thermoclines can form with temperature differences as small as 0.02°C (Imberger 1985; Shay and Gregg 1986; Imberger and Patterson 1990) and the actual frequency of near-surface thermoclines is probably higher than the one calculated in this study. For example, we found that if near-surface thermoclines were calculated from a temperature difference of 0.5°C or greater, the regression curve (in Fig. 3.1) shifts towards the X-axis (frequency is lower) while maintaining the same shape.

### Water transparency

Some of the variance in the frequency of near-surface thermoclines can be explained by differences in light penetration between lakes. In clear lakes, solar radiation penetrates farther, distributing heat to a greater depth and causing deeper thermoclines. The incidence of near-surface thermoclines increased with increasing extinction coefficient,  $K_d$  (Fig. 3.2). Even the



depth of main thermoclines is deeper in clear-water lakes than in brown water lakes, independent of lake size (Salonen et al. 1984; Perez-Fuentetaja et al. 1999; Snucins and Gunn 2000). Within individual lakes, thermocline depth increases if the water becomes clearer, as is commonly observed during prolonged periods of drought (Schindler et al. 1996a; Dillon and Molot 1997). Because of the greater radiation absorbing capacity of colored waters, heating is restricted to the surface and multiple thermoclines form more readily (Salonen et al. 1984). Mazumder and Taylor (1994) showed that water clarity explained thermocline depth of small lakes ( $<12.5 \text{ km}^2$ ) better than that of larger lakes. Fee et al. (1996) also showed that the influence of water clarity on thermocline depth diminished as lake size exceeded 500 ha. However, both mixing depth and transparency were positively correlated with lake size. Therefore the correlation between development of near-surface thermoclines and transparency ( $K_d$ ) could simply reflect the underlying relation with lake size that both variables share ( $P < 0.001$ ,  $r = 0.49$ ).

### Temperature-related density differences

Density differences per unit temperature change are greater at warm temperatures (Hutchinson 1957). This is potentially important, because larger lakes are usually colder in the summer than nearby smaller lakes (Fee and Hecky 1992; Fee et al. 1992). As expected, average water stability ( $N$ ) near the surface of the lake decreased with increasing lake size (Fig. 3.3a). The Brünt-Väisälä frequency was also related to water transparency (Fig. 3.3b,  $r^2 = 0.44$ ,  $P < 0.001$ ).

### Interannual patterns

Interannual variations in annual means of daily maximum air temperatures and daily mean wind speed might be related to the development of different annual near-surface thermocline patterns. Since 1970, average air temperature (Schindler et al. 1990, 1996a; Fee et al. 1996), wind speed (Fig. 3.4a) and water transparency (Fig. 3.4b) in northwestern Ontario have increased. We hypothesized that the increase in wind would reduce the frequency of near-surface thermoclines at the ELA. In the early 70s, when ELA lakes were surrounded by dense and mature forests (Schindler 1998), lakes had a high frequency of near-surface thermoclines (Fig. 3.4c, d). Following two major fires (in June of 1974 and 1980) and clearcutting (in the 70s and early 80s), which resulted in the partial removal of vegetation in much of the region surrounding ELA, the average wind increased (Fig. 3.4a) and the frequency of near-surface thermoclines decreased (Fig. 3.4c,d). As expected, the frequency of formation of near-surface thermoclines was inversely





related to wind speed ( $r^2 = 0.27$ ;  $P = 0.0071$ ). However, the variance explained by this relationship is low. Perhaps it is not surprising that wind explained only 27% of the variation for several reasons. Wind probably has less potential to explain the variability in near-surface thermoclines that we found, compared to lake size and water transparency. In addition, it has recently been shown that only a small fraction ( $\sim 3\%$ ) of the turbulent energy flux from wind enters the lake (Wüest et al. 2000). Furthermore, solar radiation (solar insolation and general heating) is likely a strong driver of the development of near-surface thermoclines (Imberger 1985), regardless of wind velocity. Air temperature has also been increasing in the ELA area (Schindler et al. 1996a) and this may offset the wind forcing on the mechanical development/erosion of near-surface thermoclines. Finally, the ELA experienced a drought in the 80s causing an increase in water transparency (Fig 3.4b) and deeper thermoclines (Schindler et al. 1996a). It is also possible that near-surface thermoclines were deeper than 1 m. The annual frequency of near-surface thermoclines was positively related with the annual average  $K_d$  in Fig. 3.4b ( $P < 0.05$ ;  $r^2 = 0.22$ ). Clearly, further studies are needed to assess the relative importance of solar radiation, wind, lake size, and lake clarity.

It seems that deforestation will only affect stratification patterns (e.g., thermocline depth) in small lakes ( $< 4$  ha) (Rask et al. 1993; Steedman and Kushneriuk 2000; Scully et al. 2000). Recently, Steedman and Kushneriuk (2000) found that logging does not increase wind reaching the surface of lakes 30 to 40 ha in size. Although wind measured at the ELA weather station has increased since 1970 (Fig. 3.4a), following the fires and clearcutting, it is difficult to assess whether this translated into wind changes at the lake surface. Available field wind data (after 1990) illustrate that average wind speeds at the surface of the ELA lakes increase logarithmically with surface area (Fig. 3.5). These data also show that wind speeds at the lakes surface quickly reach an upper limit ( $\sim 20$  ha). This upper limit is similar to the average wind velocity measured at the ELA meteorological station for 1990-1994. More data are clearly needed to accurately assess the influence of deforestation on wind exposure in lakes of all sizes.

## Conclusions

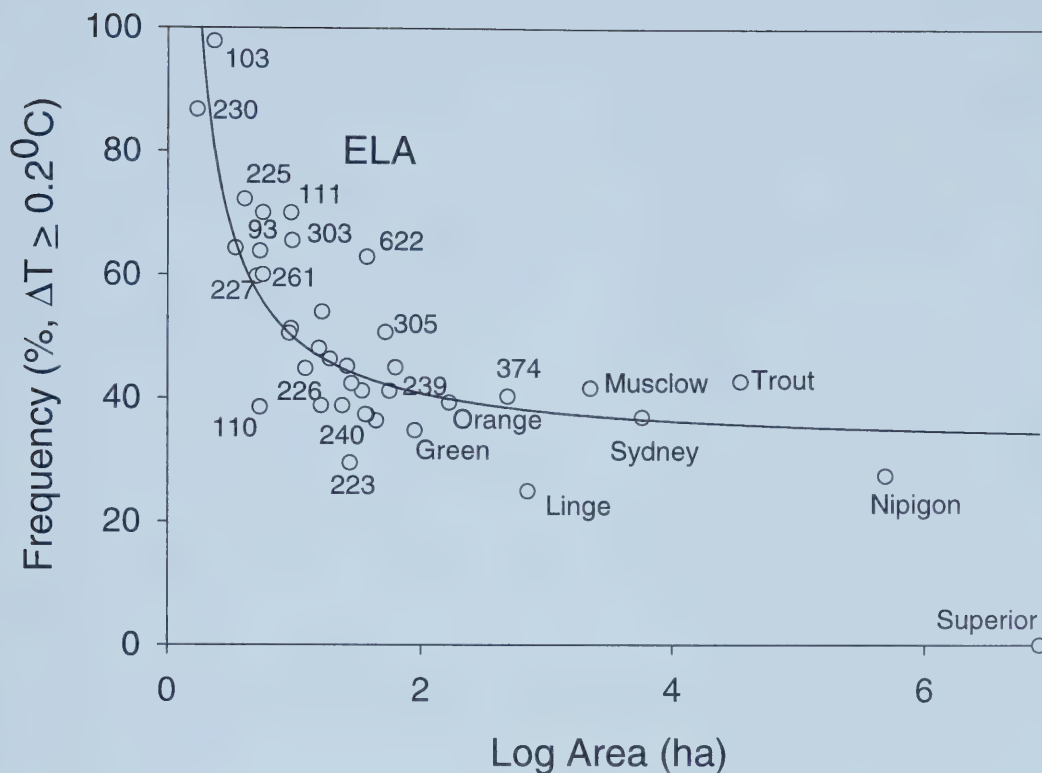
The high frequency of near-surface thermoclines indicates that they can be an important determinant of lake biology and chemistry. Williamson et al. (1996) showed that near-surface thermoclines occurred 28% of the time in a range of lakes from northeastern USA. These lakes were similar in size to the ELA lakes, but no details are given about how the presence of near-





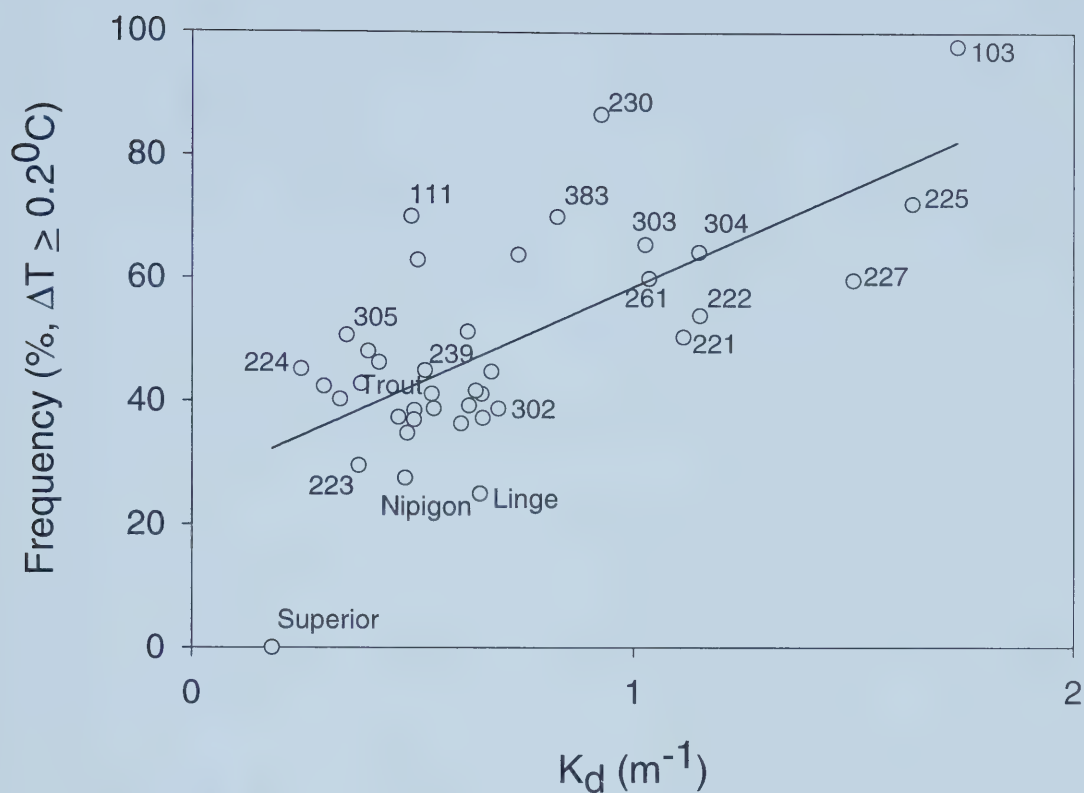
surface thermoclines was detected. We show here that the frequency of near-surface thermoclines can be much higher than 28%. In addition to the near-surface layer, which we emphasize here, more attention to deeper substrata seems important. The intensity of UV radiation and photosynthetically active radiation, intensity of turbulence and nutrient conditions can differ among sublayers (Spigel and Imberger 1987; Ivey and Imberger 1991; MacIntyre 1993). Small temperature differences within the epilimnion have usually been ignored by chemists and biologists although they affect many important ecological processes. For example, Xenopoulos et al. (2000) found significant changes in species composition of the algal community when shallow surface thermoclines and high incident UV co-occurred. Weak and transient as these thermoclines are, they are present very frequently, and can have important effects on both species assemblages and ecosystem processes in lakes of all sizes.





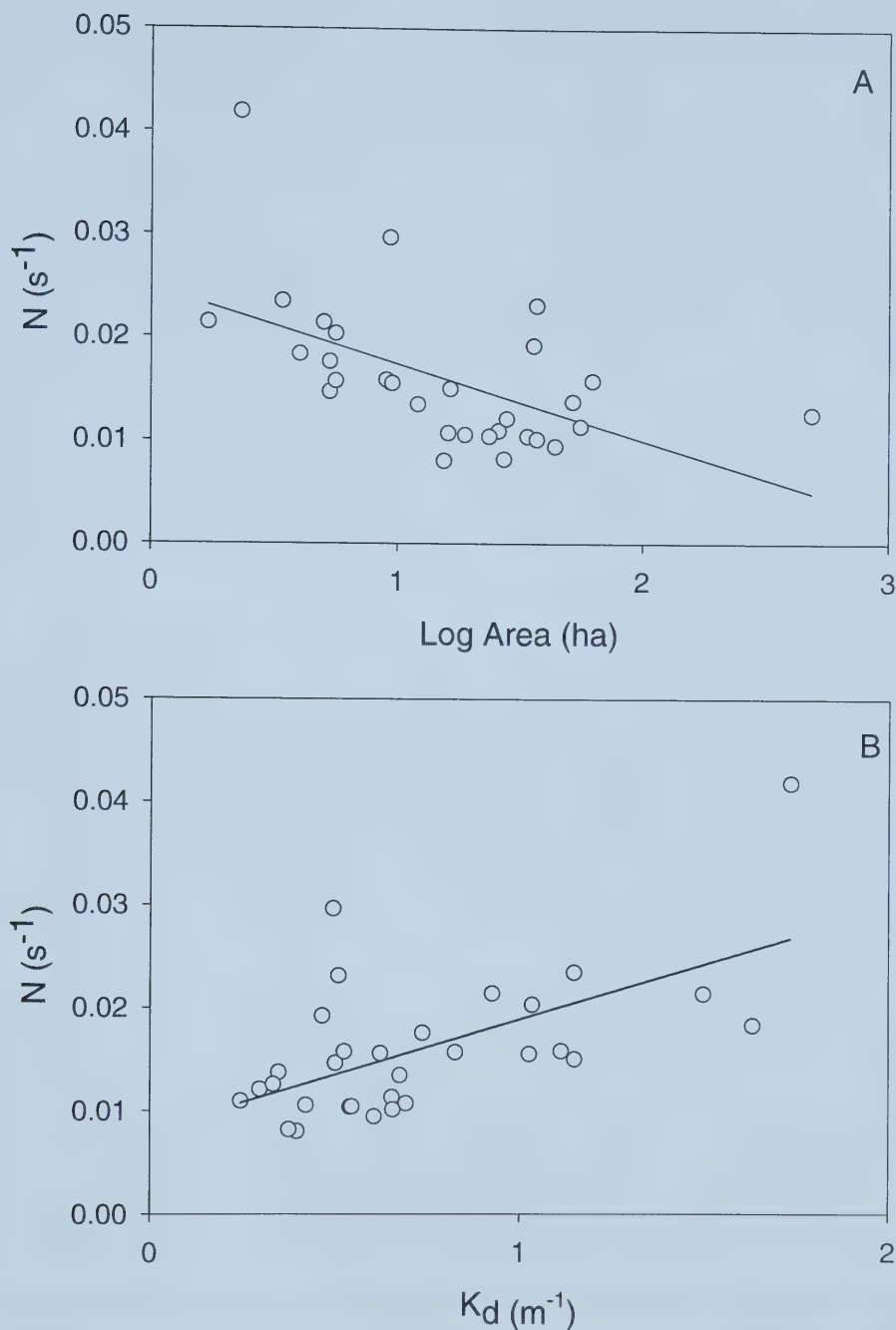
**Figure 3.1.** Frequency of secondary thermoclines in a range of lake sizes in the ELA and NOLSS. The regression is: frequency (%) =  $17.7/\log A_0 + 31.9$ ,  $r^2 = 0.60$  ( $P < 0.0001$ ). A range of statistical regression lines was tested for their ability to explain the variance in % near-surface thermoclines. The asymptotic regression model above was found to be the best fit (as determined from  $r^2$  comparisons).





**Figure 3.2.** The relationship between frequency of near-surface thermoclines ( $\%$ ,  $\Delta T \geq 0.2^\circ\text{C}$ ) and light extinction coefficient ( $K_d$ ) for the ELA and NOLSS. The regression is: frequency ( $\%$ ) =  $32.2(K_d) + 26.4$ ;  $r^2 = 0.45$  ( $P < 0.0001$ ).

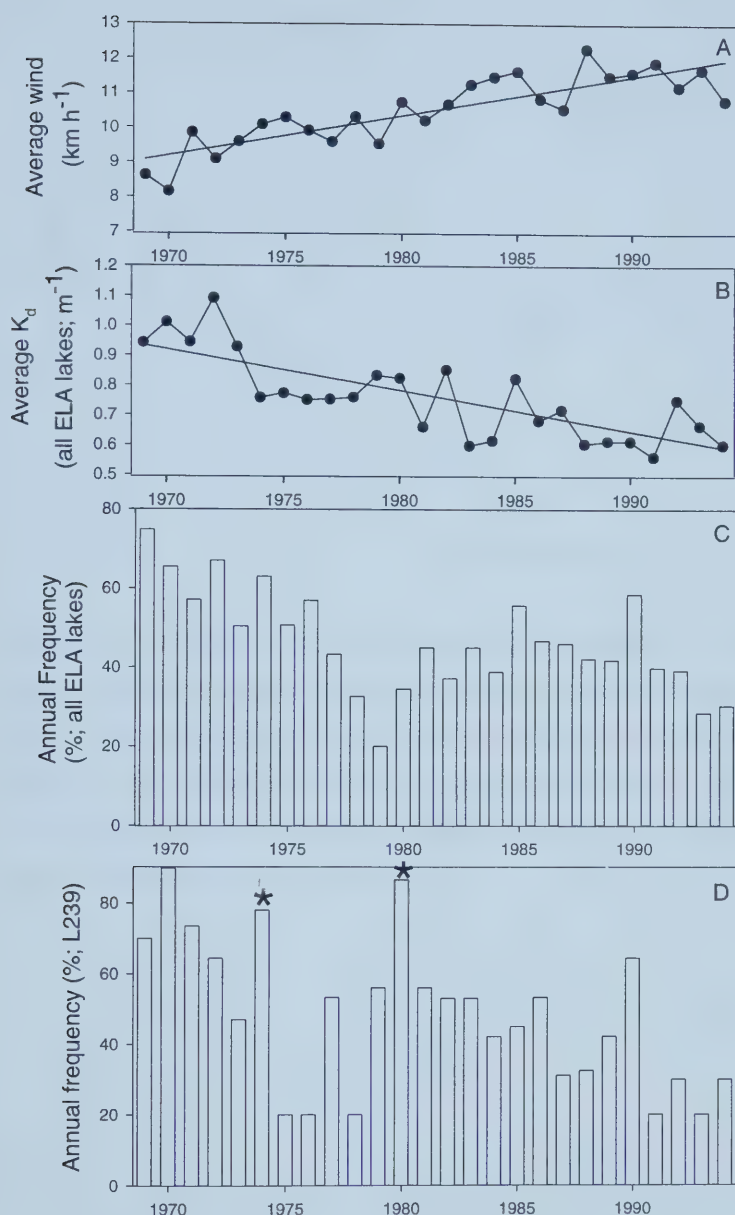




**Figure 3.3.** A) The relationship between the average Brünt-Väisälä frequency ( $N$ ) and lake size for ELA lakes.  $N$  was averaged per lake for years 1968-1994. The regression is  $N = 0.0256 - 0.0088 (\log A_0)$ ,  $r^2 = 0.39$  ( $P = 0.0004$ ). B) The relationship between  $N$  and  $K_d$ . The regression is  $N = 0.0081 (K_d) + 0.0108$ ,  $r^2 = 0.34$  ( $P = 0.0003$ ).

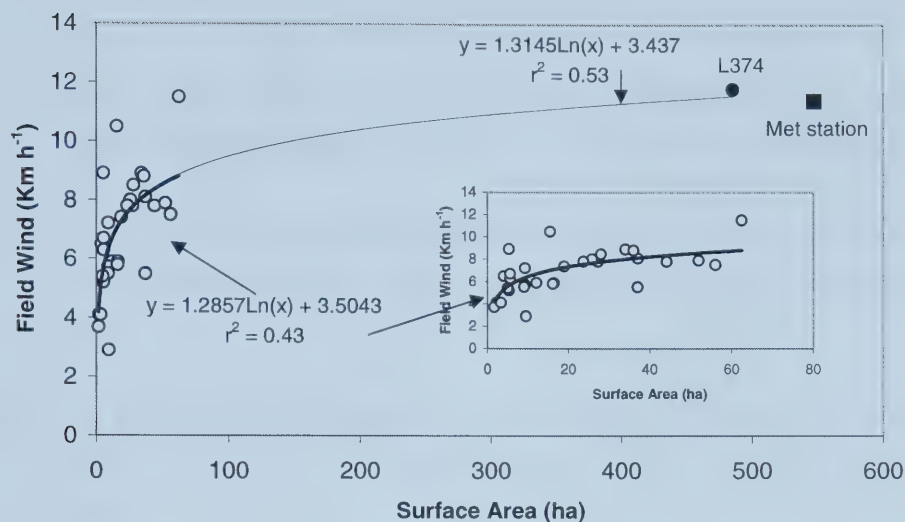






**Figure 3.4.** A) Average wind velocity at the ELA weather station during the ice-free season and linear regression line for the data. B) Yearly average  $K_d$  for all ELA lakes and linear regression line for data. C) Yearly average frequency of near-surface thermoclines for all lakes during the ice-free season at the ELA. D) Yearly average frequency of near-surface thermoclines in L239. Asterisks indicate dates of forest fires in the catchment. Two major fires occurred around the L239 watershed. The first, in late June 1974 burned over 50% of the catchment. The second, in June 1980 burned ~70% of the catchment.





**Figure 3.5.** Relationship between average wind at the lake surface (1990-1994) and lake size for lakes at the ELA, and inset, relationship between average wind speed at the lake surface and lake size for lakes smaller than 80 ha. The darker regression line does not include the outlier L374. Both regression slopes were found to be significantly equal ( $P > 0.05$ ; Analysis of Covariance). The L374 data point is approximately equivalent to the 1990-1994 average wind speed at the ELA meteorological station of  $11.4 \text{ km h}^{-1}$ .



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#### 4. JOINT EFFECTS OF ULTRAVIOLET RADIATION AND PHOSPHORUS SUPPLY ON PHYTOPLANKTON GROWTH RATE AND ELEMENTAL COMPOSITION<sup>3</sup>

##### INTRODUCTION

In aquatic ecosystems, solar radiation simultaneously affects physical, chemical and biological processes such as thermal stratification and the vertical distribution of nutrients, photoautotrophs, herbivores and consumers. While sunlight is obviously beneficial (i.e. primary producers rely on it for photosynthesis), it can also be harmful, particularly when the plankton are exposed to high intensities or damaging ultraviolet wavelengths (UVA and UVB), for prolonged periods of time (Xenopoulos et al. 2000). Another key factor in aquatic systems is the supply and relative availability of nutrients, which strongly affect planktonic algal biomass, productivity, and species composition (Schindler 1977). While studies have examined the individual effects of ultraviolet radiation (UVR) and nutrients on algal growth, the extent and nature of the interaction between these two abiotic factors remains relatively unknown. In light of recent connections established among multiple stressors (e.g. Folt et al. 1999, Frost et al. 1999, Leavitt et al. 1999), the knowledge of these interactive effects is especially needed. The objective of this study was to determine the influence of UVR under different conditions of phosphorus (P) supply on the growth rates and elemental composition of natural phytoplankton communities in two boreal lakes.

Perhaps the most studied effect of UVR on primary producers is the inhibition of photosynthesis due to photosystem damage (e.g. Schofield et al. 1995, Nilawati et al. 1997) and bleaching of photopigments. Reduced rates of carbon fixation from high UVR imply lower rates of algal growth, although plankton ecologists are becoming increasingly cautious of this link (Berman-Frank and Dubinsky 1999). To date, what little is known about the influence of UVR on algal growth kinetics is based on laboratory work, mainly with cultured species (Calkins and Thordardottir 1980, Jokiel and York 1984, Nilawati et al. 1997, West et al. 1999). Furthermore, little is known about how sensitivity of algal growth to UVR may be influenced by the cell's

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<sup>3</sup> A version of this manuscript has been accepted for publication: Xenopoulos, M.A., P.C. Frost and J.J. Elser. Joint effects of ultraviolet radiation and phosphorus supply on phytoplankton growth rate and elemental composition. *Ecology*, in press.



nutrient status. In particular, nutrient-deficient phytoplankton may respond differently to UVR than phytoplankton not otherwise under nutrient-stress (Bergeron and Vincent 1997). We hypothesize that there would be an interactive effect of ultraviolet radiation and nutrients on growth rates of natural phytoplankton communities.

In general, growth rates of aquatic photoautotrophs reflect the many environmental conditions that affect photosynthesis and nutrient-uptake. Temperature, photosynthetically active radiation (PAR), and nutrients are most often considered the ecologically important factors that control algal growth rates in lakes (e.g. Sterner and Grover 1998). However, the influence of sunlight quality (UVA, UVB and PAR) on *in situ* rates of algal growth remains poorly studied.

Not much is known about the influence of natural levels of UVR on elemental composition of phytoplankton. Changes in algal growth rates can lead to major changes in cellular biochemistry and hence, elemental composition (Healey and Hendzel 1979, Kilham et al. 1997). Consequently, there is an intimate interplay between light, nutrients, and elemental composition in primary producers (Rhee and Gotham 1981, Nielsen et al. 1996, Sterner et al. 1997). PAR affects algal elemental ratios by altering the balance of net photosynthesis to nutrient uptake (Sterner et al. 1997). Increasing PAR at one level of nutrient supply increases rates of gross photosynthesis, which can result in increased algal C:P ratios in laboratory cultures (Rhee and Gotham 1981, Goldman 1986). Thus, one might imagine that UVR could affect algal C:N:P ratios by reducing rates of net C-fixation due to lower rates of photosynthesis and increased respiratory loss of carbon. In addition, UVA and UVB may decouple photosynthetic processes and cell division, leading to increased cell volume (Karentz et al. 1991). This, in turn, may promote accumulation of intracellular carbon-rich compounds and a subsequent increase in cellular C:P ratios (Van Donk and Hessen 1995).

UVR may also influence algal elemental composition by altering nutrient uptake mechanisms. Reduced uptake rates of nitrate, ammonium and phosphorus from UVR exposure have been reported (Döhler 1985, Behrenfeld et al. 1995, Hessen et al. 1997). Other laboratory work has shown that at high doses of UVB phosphate uptake is strongly inhibited whereas at low UV doses there is an increase in P uptake by algae (Hessen et al. 1995). This latter increase could be due to an increased demand for phosphorus to replace cell constituents injured by UVB (e.g. nucleic acids) or to provide metabolites needed for cell repair (e.g. ATP).



Changes in autotroph elemental composition affect biogeochemical processes (Elser and Urabe 1999) and food web dynamics (Sterner et al. 1992). In particular, accumulating evidence suggests that P-limited cells are poor food for zooplankton, especially P-rich taxa like *Daphnia* (Sterner et al. 1993, Elser et al. in press). Biochemical properties of phytoplankton altered by UVR could also affect herbivores by altering digestibility and biochemical nutritional quality (Hessen et al. 1997; De Lange and Van Donk 1997). Indeed, *Daphnia pulex* fed UVB-irradiated algae had decreased survival and fecundity (Scott et al. 1999).

In this paper, we examine the effects of UVA, UVB and PAR on the growth and elemental composition of phytoplankton at different levels of phosphorus supply. We used dilution bioassays in two different lakes throughout the summer of 1999 to determine whether UVR would alter the growth responses of phytoplankton to phosphorus. We show here that ambient UVR exerts a strong influence on phytoplankton growth rates and physiological condition under natural conditions but the magnitude of this effect changes during the summer growing season.

## METHODS

### Study sites

This study was conducted in two lakes at the Experimental Lakes Area (ELA), situated in the boreal forest of northwestern Ontario, Canada (49°40'N, 93°44'W). Lake 224 (L224) is one of the clearest lakes (PAR extinction coefficient ( $K_{dPAR}$ ) = 0.3 m<sup>-1</sup>) at the ELA with a surface area of 25.9 ha, a maximum depth of 27 m and a mixing depth of ~6 m. Low dissolved organic carbon (DOC) concentrations (~3 mg L<sup>-1</sup>) and high UVB penetration (1%, ~1.5 m) characterize this lake (Schindler et al. 1996). Dominant algae are chrysophytes such as *Dinobryon*, *Uroglena* and *Chrysochromulina* and diatoms such as *Tabellaria*. Lake 302's (L302) two basins have been separated by a vinyl curtain since 1981. The south basin (L302S) has a surface area of 10.9 ha, a maximum depth of 10 m and a mixing depth of ~3 m. L302S has been artificially acidified since 1982. The pH was reduced from 6.7 (1982) to 4.5 (1989-1991). The lake has been recovering since 1992 and the pH has been held at 6.0 since 1996 (Findlay et al. 1999). Many chemical and biological changes followed lake acidification, some of which are UVR-related. First, DOC concentration was significantly reduced to < 1 mg L<sup>-1</sup> (Schindler et al. 1996) and DOC quality altered, increasing UV penetration by 800% (Donahue et al. 1998). Second, the concentration of UV-protective pigments increased (Leavitt et al. 1999). Finally, chrysophytes and diatoms,





naturally present in the lake before acidification, were replaced with filamentous greens and dinoflagellates (Findlay et al. 1999, Leavitt et al. 1999). In 1999, the average DOC concentration in this lake was  $4.5 \text{ mg L}^{-1}$  (1% UVB penetration,  $\sim 0.75 \text{ m}$ ;  $K_{d\text{PAR}} = 0.6 \text{ m}^{-1}$ ).

### **Dilution bioassays and UV-manipulations**

Phosphorus (P) is the primary limiting nutrient controlling algal growth in lakes at the ELA (Schindler 1977). Dilution bioassays were used to examine the responses of algal growth rate to P additions under three light regimes incubated in the lakes using 1.2 L Whirlpak polyethylene bags (NASCO plastics, Burlington, Ontario, Canada) placed inside floating wire baskets ( $\sim 50 \text{ cm}$  depth). Whirlpak bags transmit solar radiation at wavelengths  $>220 \text{ nm}$  (Prézelin and Smith 1992). Five phosphorus concentrations and three light treatments were applied: 1) ambient radiation (PAR + UVA + UVB), 2) PAR + UVA, and 3) PAR only. Light treatments were produced using plastic sheets (Cadillac Plastics, Winnipeg, Manitoba, Canada) that block different wavelengths: OP-3 (50% sharp cutoff =  $400 \text{ nm}$ , transmitting PAR only); OP-4 (50% cutoff =  $280 \text{ nm}$ , transmitting UVB, UVA and PAR); Mylar-D (50% sharp cutoff =  $318 \text{ nm}$ , transmitting UVA and PAR). Spectral transmittance characteristics were confirmed with a Li-Cor Model LI-1800UM Spectroradiometer (see Vinebrooke and Leavitt 1999 for more details on spectra).

Growth bioassays were repeated three times in L224 (early spring, summer solstice, and late summer) and twice in L302S (summer solstice and late summer; Table 4.1). Our approach was modified from Sterner and Grover (1998) and Sterner (1994). A portion of the lake water sample (sampled at  $0.5 \text{ m}$ ) was filtered through a  $0.2 \mu\text{m}$  pore-size, polycarbonate filter. This filtered water was added in different proportions (Table 4.1) to the original whole lake water that was screened through  $80 \mu\text{m}$  mesh Nitex to remove large metazoan grazers. Dilution of the sample is designed to reduce the effects of microzooplankton grazing (Sterner and Grover 1998) and competition for nutrients, permitting a more direct estimation of algal growth rates. Water samples were then supplied with 5 different concentrations of phosphorus (Table 4.1) and  $650 \mu\text{g L}^{-1}$  of nitrogen and incubated for 72 hours. P-additions varied depending on the experiment and lake (Table 4.1). Except for experiment 1 (where we followed the protocol in Sterner and Grover (1998)), we varied the dilution ratios and phosphorus additions between L302S and L224 in subsequent experiments to reflect the differences in phytoplankton biomass and nutrient concentrations. Triplicate bags were used for each treatment combination. After 72 hours,





lakewater in the bags were processed for chlorophyll *a* (Chl) after extraction in boiling ethanol (Nusch 1980). Seston carbon was collected on a GF-C filter (pore size  $\sim 1\mu\text{m}$ ) and was estimated using an infrared analyzer (O.I. Corporation, Model 700) after digestion with potassium persulfate (Strickland and Parsons 1972, Sterner et al. 1993). Seston phosphorus was estimated on the same digested sample using the molybdate-ascorbic acid method (APHA 1992).

**Table 4.1.** Date, lake, phosphorus additions (five-levels), dilution ratio (filtered water: whole lake water), average (3-day) surface UVB and UVA daily doses and daily surface PAR (3-day average) for each of the dilution growth bioassays. In parentheses are the average daily doses of UVB, UVA and PAR corrected for lake attenuation (0.50 m depth).

Exp no	Lake	Date (in 1999)	P $\mu\text{g L}^{-1}$	dilution ratio	UVB $\text{kJ m}^{-2}\text{d}^{-1}$	UVA $\text{kJ m}^{-2}\text{d}^{-1}$	PAR $\text{Ein m}^{-2}\text{d}^{-1}$
1	L224	Spring, May 20-23	0, 2, 10, 20, 200	80:20	25.7 (5.21) <sup>†</sup>	600.0 (270.3) <sup>†</sup>	32.8 (28.2)
2	L302S	Summer solstice, June 18-21	0, 2, 12, 20, 100	60:40	52.9 (1.78)	1140.0 (255.5)	43.7 (32.4)
3	L224	Summer solstice, June 22-25	0, 2, 10, 20, 60	40:60	64.6 (13.1)	1245.7 (561.1)	48.1 (41.4)
4	L302S	Late summer, July 27-30	0, 2, 10, 20, 100	60:40	65.9 (2.22)	1303.8 (292.3)	58.4 (43.3)
5	L224	Late summer, August 4-7	0, 2, 10, 20, 60	40:60	52.8 (10.7)	1055.6 (475.5)	42.8 (36.9)

Note: <sup>†</sup> UVB and UVA in lake were calculated using attenuation equations from Scully and Lean (1994).

### Solar radiation measurements

Incident surface UVA and UVB were measured at regular intervals (10-min intervals) with wide-band UVA (320-400 nm) and UVB (280-320 nm) sensors (BW20 Vital Technologies) attached to a Li-Cor data logger (output in Volts) and cross-calibrated with a Li-Cor Model LI-1800UM Spectroradiometer (output in  $\text{W m}^{-2}$ ). Daily surface PAR was measured at 1-second intervals using a Li-Cor quantum sensor. Surface UVR and PAR measurements were made at the ELA meteorological station located  $\sim 2.5$  km from the lakes. All experiments began during cloudless or near cloudless days. UVR values throughout our experiments were typical of (or close to) the maximum found during the season in this geographical area. Average UVA and UVB total daily



doses and average daily PAR measurements are presented in Table 4.1. UVA and UVB dose rates throughout the five experiments are shown in Fig. 4.1.

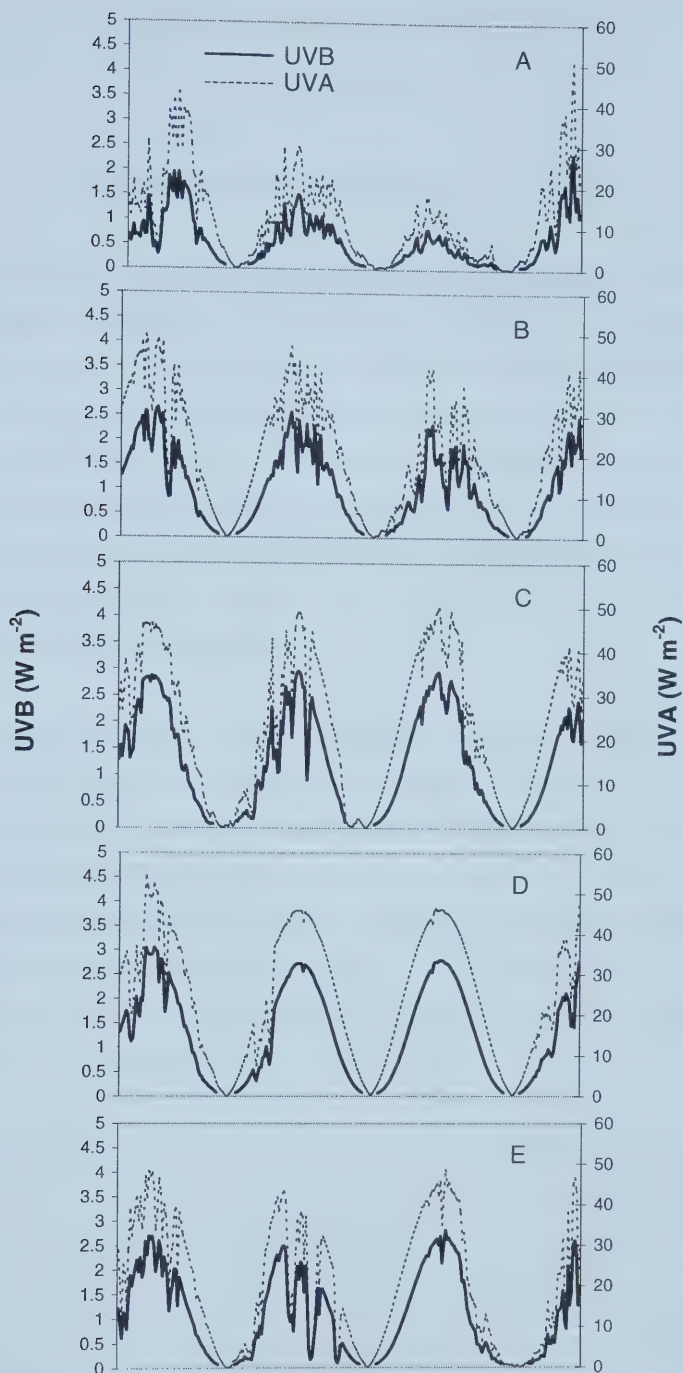
## Data analysis

Growth rates of seston C and Chl were calculated assuming exponential growth. Non-linear regression was then used to fit growth rates with P concentrations following Monod (1950) growth kinetics:

$$\mu = \mu_{\max} \frac{P}{(P + K_s)}$$

where  $\mu$  is the growth rate,  $\mu_{\max}$  is the maximum growth rate at the saturating phosphorus concentration and  $K_s$  is the concentration at which growth rate is one half its maximum (half saturation constant). Estimates of  $K_s$  and  $\mu_{\max}$ , along with their respective 95% confidence intervals, were determined using the non-linear fitting component of JMP (SAS Institute 1996).  $K_s$  and  $\mu_{\max}$  values for different light treatments were compared by examining the resulting 95% confidence intervals. Effects of light and phosphorus treatments on growth rates, C:P and C:Chl ratios were evaluated with two-way analysis of variance. Preliminary results showed that significant interaction effects of phosphorus and light treatments were common. Hence, significance between light treatments was further assessed with Tukey-Kramer multiple comparison tests for each of the phosphorus levels. Significant differences are reported at the 0.05 probability level.





**Figure 4.1.** Surface UVA (320-400 nm) and UVB (280-320 nm) dose rates ( $\text{W m}^{-2}$ ) for experiments 1 to 5 (A to E respectively) as in Table 4.1 for the whole duration of the experiment. Measurements are from 9 AM on the first day until noon on the last day.



## RESULTS

### UVR influence on Chlorophyll growth rates and seston C growth rates

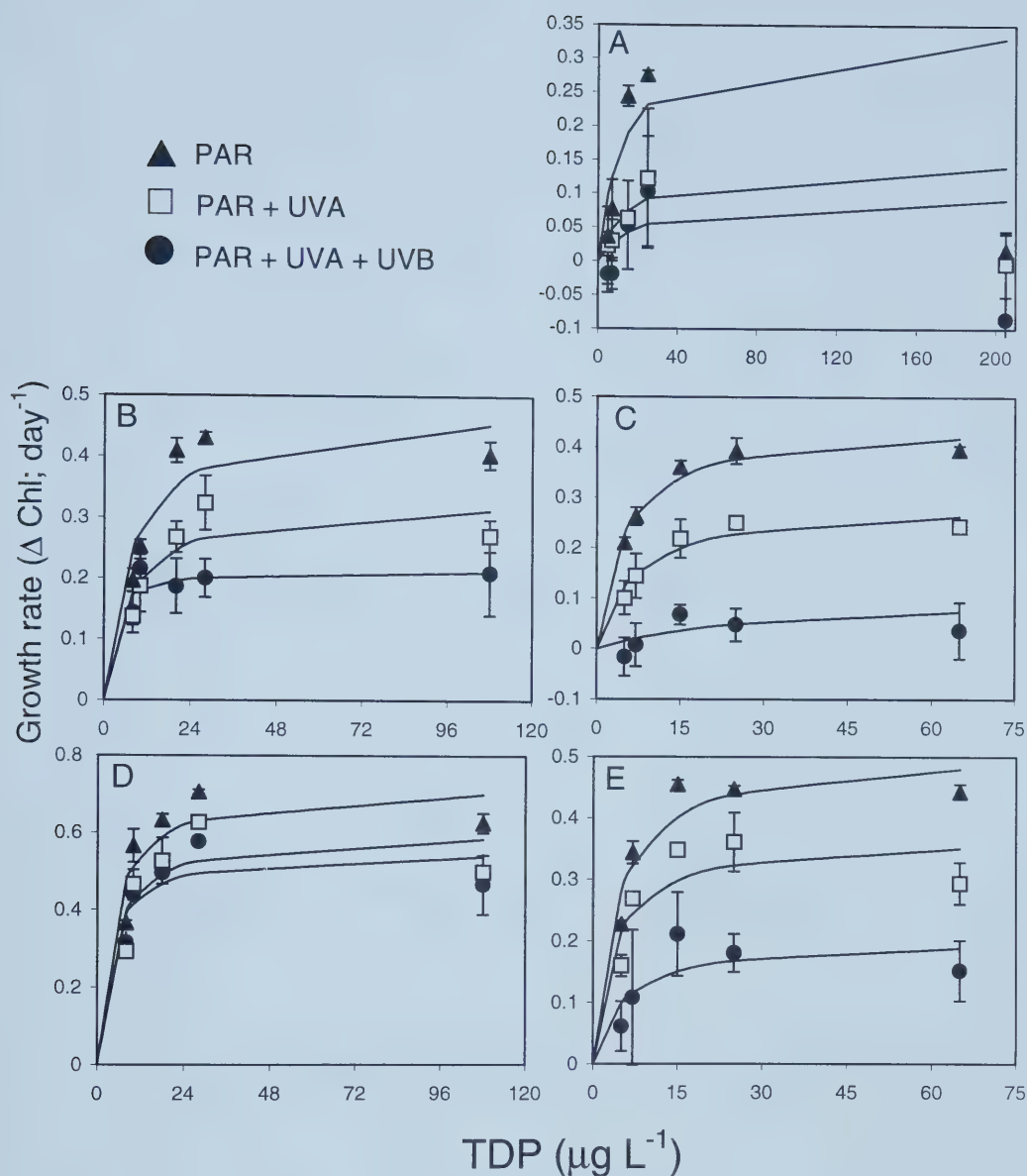
Phytoplankton exposed to UVA and UVB grew more slowly than those exposed to PAR only, as assessed by changes in chlorophyll (Fig. 4.2) and seston C (Fig. 4.3). The magnitude of reduction depended on the time and the lake where the experiment was performed. The magnitude of the UVA and UVB effect on chlorophyll growth rates was not always the same as that on growth as measured by seston C (Fig. 4.2 and 4.3). Growth rates calculated from changes in chlorophyll were more variable than those calculated from changes in seston C. Nevertheless, seston carbon and chlorophyll growth rates were always positively correlated, although this correspondence was not always high ( $r^2$  values for experiments 1 through 5 were: 0.17, 0.67, 0.63, 0.80 and 0.36 respectively;  $P < 0.05$  for all experiments).

In the first experiment, the highest P addition inhibited chlorophyll growth (fig 4.2a). The maximum P addition was reduced in subsequent experiments. In L302S, the algal population sampled during the summer solstice was more sensitive to UVB than those sampled later in summer (Fig. 4.2b, d; Fig. 4.3b, d). In fact, in late summer, there was no influence of UVB on seston C growth rates in L302S (Fig. 4.3d). In L224, UVA and UVB equally inhibited algal growth as calculated from chlorophyll changes (Fig. 4.2a, c, e). However, in the June experiment in L224, the phytoplankton were considerably more sensitive to UVB than in late summer, as indicated from seston C-growth rates (Fig. 4.3c, e).

Both phosphorus enrichment and light treatments always had a significant effect on chlorophyll and seston C growth rates (Table 4.2). A significant interaction effect ( $P \times \text{light}$ ) was detected in three out of the five experiments (Table 4.2), although not always in the same experiment for growth rates calculated from carbon and chlorophyll. Except for experiment 4 (L302S, late summer), light treatment explained a higher proportion of the variance in chlorophyll and seston C growth rates than did P enrichment (Table 4.2).

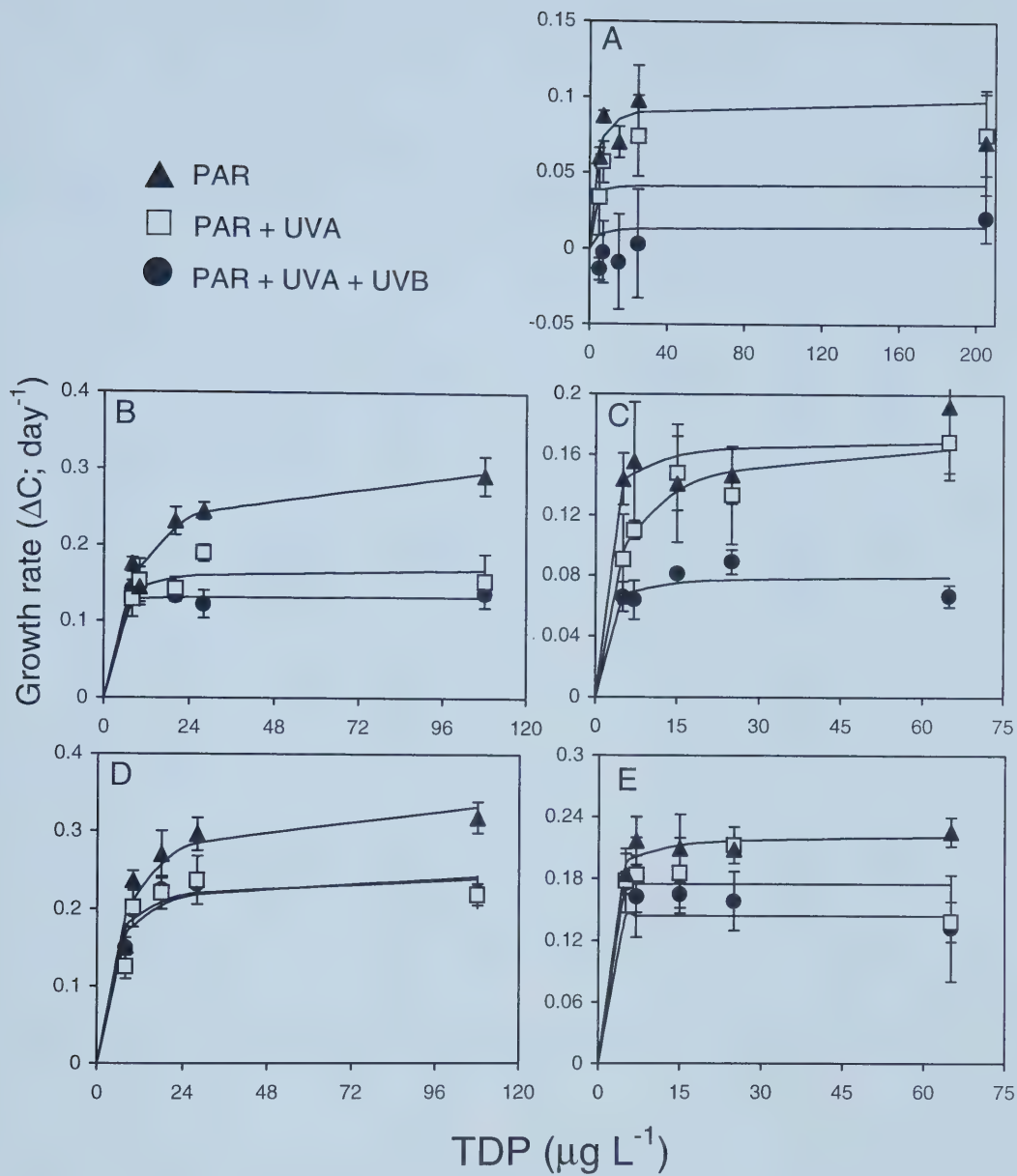






**Figure 4.2.** The Monod phosphorus-dependent chlorophyll growth curves, determined using non-linear regression in three different light regimes for A to E, experiments 1 to 5 respectively as in Table 4.1. Error bars are standard deviations. Note: the X and Y-axis vary among panels. In A) growth curve was determined assuming saturation of growth at P-level 4 (20  $\mu\text{g L}^{-1}$ ).





**Figure 4.3.** The Monod phosphorus-dependent seston carbon growth curves in three different light regimes for A to E, experiments 1 to 5 respectively as in Table 4.1. Error bars are standard deviations. Note: the X and Y-axis vary among panels.



**Table 4.2.** Two-way analysis of variance for the effects of phosphorus and sunlight on the chlorophyll and seston C growth rates. Experiment numbers as in Table 4.1.

Exp.	Source	DF	Chlorophyll			Seston C		
			F	P	% variance <sup>†</sup>	F	P	% variance
1	Model	14	8.4790	<0.0001	80.9	7.7054	< 0.0001	78.3
	P	4	16.4261	<0.0001	24.6	4.8556	0.0039	14.1
	Light	2	18.0371	<0.0001	44.8	37.8211	<0.0001	54.8
	Light × P	8	1.3553	0.2585	7.4	1.662	0.1662	9.3
	Error				19.1			21.7
2	Model	14	24.8496	<0.0001	92.1	22.0119	<0.0001	91.9
	P	4	35.2496	<0.0001	37.3	12.8310	<0.0001	15.3
	Light	2	77.2876	<0.0001	40.9	78.9460	<0.0001	47.1
	Light × P	8	6.5400	<0.0001	13.8	9.5354	<0.0001	22.7
	Error				7.9			8.1
3	Model	14	70.8407	<0.0001	97.2	8.1874	<0.0001	79.3
	P	4	42.9125	<0.0001	16.8	3.7318	0.0140	10.3
	Light	2	386.619	<0.0001	75.8	42.7409	<0.0001	59.1
	Light × P	8	2.4584	0.0363	1.9	1.7767	0.1214	9.8
	Error				2.8			20.7
4	Model	14	35.8896	<0.0001	94.5	19.5046	<0.0001	90.1
	P	4	98.0597	<0.0001	73.7	47.2504	<0.0001	62.4
	Light	2	50.2318	<0.0001	19.9	31.6697	<0.0001	20.9
	Light × P	8	1.2189	0.3219	1.8	2.5904	0.0279	6.8
	Error				5.5			9.9
5	Model	14	111.0342	<0.0001	92.8	12.3555	<0.0001	59.7
	P	4	125.9831	<0.0001	30.1	5.3860	0.0005	7.4
	Light	2	505.7443	<0.0001	60.4	48.9478	<0.0001	33.7
	Light × P	8	4.8822	<0.0001	2.3	6.6617	<0.0001	18.4
	Error				7.2			40.3

Note: <sup>†</sup> % variance calculated as: sums of squares of treatment / total sums of squares.



Results from the Tukey-Kramer multiple comparisons also show differential effects of P-concentrations on growth in the different light treatments (Table 4.3). Phytoplankton sensitivity to UVB increased with higher P (Table 4.3). Phytoplankton from L302S (exp. 2, 4) were consistently less affected by UVB and UVA than phytoplankton from L224 (exp. 1, 3, 5). At the ambient P-concentration (no P addition), there was no effect of light treatment on seston C-growth except in Experiments 1 and 3 in L224. Excluding Experiment 1, both UVA and UVB significantly reduced Chl-growth at the ambient P-level in L224 (Table 4.3). At the ambient P-concentrations, phytoplankton growth was co-regulated by P-limitation and UVR-inhibition such that in following P addition, control of algal growth appears to shift from P-limitation to UVR-suppression (Fig. 4.2, 4.3 and Table 4.3).

Maximum growth rates increased in all experiments from spring until late summer, probably due to increases in lake temperature (Table 4.4a, b). UVB reduced  $\mu_{\max}$  by 8 – 66% while UVA caused an additional reduction of 11 – 21 % (Table 4.4a, b). No significant differences were found in the half-saturation constants, which were highly variable (Table 4.4a, b). High variation in  $K_s$  estimates have been found previously (Grover 1989).

#### **UVR influence on algal C:P and C:Chl.**

P additions and UVR significantly reduced C:P ratios in phytoplankton (Fig. 4.4, Table 4.5), except in Experiment 1, where UVB increased C:P ratios and Experiment 5, where UVR had no effect (Fig. 4.4). 2-way ANOVAs revealed that P-enrichment significantly decreased sestonic C:P ratios (Table 4.5). Except for Experiment 1, P treatment explained a higher percent of variation in C:P ratios than light (Table 4.5), opposite to what was found for phytoplankton growth rates (Table 4.2).

Light treatments and phosphorus enrichment always had a significant effect on the seston C:Chl ratio (Table 4.5) but no interactions were observed. P additions decreased C:Chl ratios (not shown), while C:Chl ratios were higher in treatments exposed to the full solar spectrum relative to those exposed to PAR only (not shown). The pronounced increase of C:Chl at inhibitory light may indicate algal photoadaptation and/or photobleaching of Chl from UVR.





**Table 4.3.** Results from the Tukey-Kramer, HSD ( $\alpha = 0.05$ ) multiple comparison test of each phosphorus level (1 to 5 as in Table 4.1) between light treatments. Different letters indicate light treatments that differed significantly within each phosphorus level (the table has to be read vertically). Experiment numbers as in Table 4.1.

Exp.#	Light	Phosphorus Level									
		Chlorophyll					Seston C				
		1	2	3	4	5	1	2	3	4	5
1	PAR + UVA + UVB	a	a	a	a	a	a	a	a	a	a
	PAR + UVA	a	ab	ab	a	a	b	b	a	ab	a
	PAR	a	b	b	a	a	b	b	a	b	a
2	PAR + UVA + UVB	a	a	a	a	a	a	a	a	a	a
	PAR + UVA	a	a	b	b	a	a	a	a	b	a
	PAR	a	a	c	c	b	a	a	b	c	b
3	PAR + UVA + UVB	a	a	a	a	a	a	a	a	a	a
	PAR + UVA	b	b	b	b	b	a	ab	ab	ab	b
	PAR	c	c	c	c	c	b	b	b	b	b
4	PAR + UVA + UVB	a	a	a	a	a	a	a	a	a	a
	PAR + UVA	a	a	a	b	a	a	a	a	a	a
	PAR	b	b	b	c	a	a	a	a	b	b
5	PAR + UVA + UVB	a	a	a	a	a	a	a	a	a	a
	PAR + UVA	b	ab	b	b	b	a	a	a	b	b
	PAR	c	b	c	c	c	a	a	a	b	b



**Table 4.4.** Monod growth parameters:  $\mu_{\max}$  and  $K_s$  and their respective upper and lower 95% confidence intervals for growth kinetics calculated from a) chlorophyll changes and b) seston carbon changes. Experiment numbers as in Table 4.1.

a) Chl growth kinetics

#	Light	$\mu_{\max}$ $d^{-1}$	Lower C.I.	Upper C.I.	$K_s$ $\mu g L^{-1} d^{-1}$	Lower C.I.	Upper C.I.
1 <sup>†</sup>	PAR+UVA+UVB	0.100	-0.001	nd <sup>‡</sup>	20.568	nd	nd
	PAR + UVA	0.150	0.041	nd	15.509	nd	nd
	PAR	0.350	0.259	nd	12.717	6.170	nd
2	PAR+UVA+UVB	0.215	0.169	0.270	2.036	-1.110	7.110
	PAR + UVA	0.333	0.272	0.404	7.145	2.899	13.434
	PAR	0.485	0.417	0.562	7.784	4.264	12.543
3	PAR+UVA+UVB	0.109	0.032	nd	30.736	1.654	nd
	PAR + UVA	0.291	0.245	0.347	6.878	3.648	11.804
	PAR	0.450	0.419	0.482	4.872	3.668	6.303
4	PAR+UVA+UVB	0.554	0.472	0.646	3.417	0.859	6.852
	PAR + UVA	0.606	0.504	0.722	4.279	1.184	8.640
	PAR	0.726	0.631	0.831	4.246	1.773	7.472
5	PAR+UVA+UVB	0.203	0.129	0.317	5.292	0.040	20.499
	PAR + UVA	0.369	0.309	0.439	3.615	1.263	6.899
	PAR	0.510	0.459	0.567	4.094	2.505	6.146

Notes: <sup>†</sup> Because of growth inhibition at P-level 5 ( $200 \mu g L^{-1}$ ),  $\mu_{\max}$  and  $K_s$  were calculated assuming saturation of growth at P-level 4 ( $20 \mu g L^{-1}$ ) for Experiment 1 and confidence intervals were sometimes not determined.

<sup>‡</sup> Not determined.

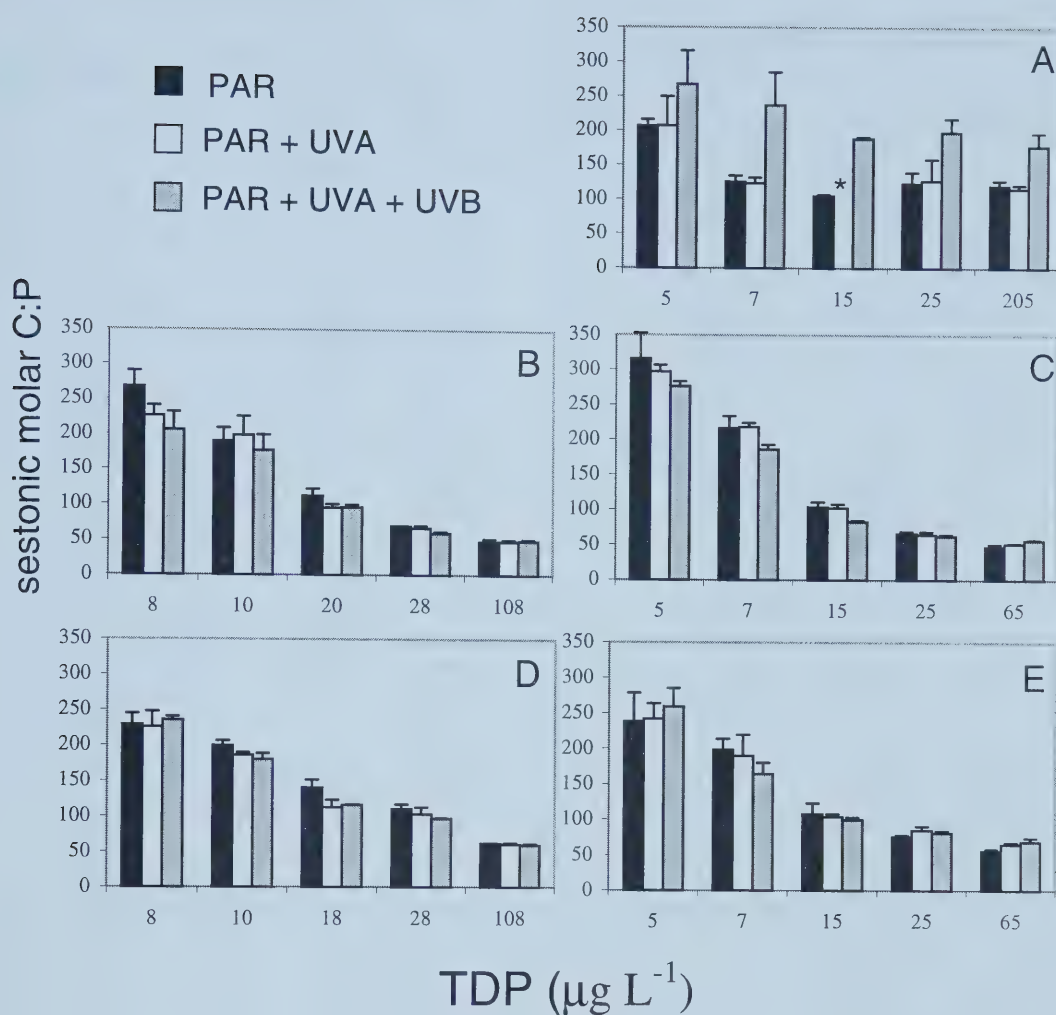


Table 4.4 continued.

## b) Seston C growth kinetics

#	Light	$\mu_{\max}$ $\text{d}^{-1}$	Lower C.I.	Upper C.I.	$K_s$ $\mu\text{g L}^{-1} \text{d}^{-1}$	Lower C.I.	Upper C.I.
1	PAR + UVA + UVB	0.020	nd	nd	3.480	nd	nd
	PAR + UVA	0.043	0.006	nd	0.775	-4.392	nd
	PAR	0.099	0.074	0.137	2.385	-0.271	7.792
2	PAR + UVA + UVB	0.132	0.121	0.144	0.219	-0.938	1.627
	PAR + UVA	0.171	0.142	0.204	1.812	-0.687	5.373
	PAR	0.319	0.287	0.355	8.891	5.936	12.584
3	PAR + UVA + UVB	0.081	0.069	0.093	1.1189	-0.288	3.072
	PAR + UVA	0.171	0.137	0.213	1.113	-0.834	4.459
	PAR	0.175	0.146	0.209	4.284	1.697	8.349
4	PAR + UVA + UVB	0.246	0.218	0.276	3.241	1.287	5.691
	PAR + UVA	0.250	0.212	0.293	4.110	1.272	7.999
	PAR	0.352	0.312	0.397	6.721	4.020	10.159
5	PAR + UVA + UVB	0.144	0.119	0.172	~0	-1.977	0.564
	PAR + UVA	0.175	0.148	0.209	~0	-1.498	1.547
	PAR	0.223	0.203	0.245	0.769	-0.111	1.860





**Figure 4.4.** Changes in C:P ratios as a function of total dissolved phosphorus in the three different light regimes for A to E, experiments 1 to 5 respectively as in Table 4.1. Error bars are standard deviations. (\*) not determined.





**Table 4.5.** Two-way ANOVA for the influence of phosphorus and light levels on C:P and C:Chl ratios. Experiment numbers as in Table 4.1.

Exp.	Source	DF	C:P			C:Chl		
			F	P	% variance <sup>†</sup>	F	P	% variance
1	Model	14	13.5452	<0.0001	86.3	3.6524	0.0014	63.0
	P	4	16.8835	<0.0001	30.7	3.9255	0.0111	19.3
	Light	2	35.6256	<0.0001	32.4	16.7082	<0.0001	41.2
	Light × P	8	6.3560	<0.0001	23.1	0.2518	0.9765	2.5
	Error				13.7			37.0
2	Model	14	77.9771	<0.0001	97.4	7.2314	<0.0001	77.8
	P	4	270.4044	<0.0001	96.5	15.3946	<0.0001	47.2
	Light	2	7.0626	0.0032	1.3	10.8813	0.0003	16.7
	Light × P	8	2.2475	0.0528	1.6	1.6583	0.1517	10.1
	Error				2.6			22.2
3	Model	14	215.0648	<0.0001	99.0	16.4419	<0.0001	88.5
	P	4	742.8094	<0.0001	97.7	9.4536	<0.0001	14.5
	Light	2	9.3450	0.0007	0.6	93.5884	<0.0001	71.9
	Light × P	8	2.6225	0.0263	0.7	0.6494	0.7303	2.0
	Error				1.0			11.5
4	Model	14	144.6481	<0.0001	98.5	13.6565	<0.0001	86.4
	P	4	498.9318	<0.0001	97.1	15.2960	<0.0001	71.3
	Light	2	6.8178	0.0036	0.7	15.2960	<0.0001	13.8
	Light × P	8	1.9638	0.0866	0.8	0.3476	0.9395	1.3
	Error				1.5			13.6
5	Model	14	55.0722	<0.0001	96.4	15.9065	<0.0001	89.9
	P	4	189.8963	<0.0001	94.9	25.9558	<0.0001	41.9
	Light	2	0.0891	0.9150	0	54.6232	<0.0001	44.1
	Light × P	8	1.3561	0.2567	1.4	0.4912	0.8508	1.6
	Error				3.6			10.1

Note: <sup>†</sup> % variance calculated as: sums of squares of treatment / total sums of squares.



## DISCUSSION

### UVR effects on phytoplankton growth in boreal lakes

We found negative effects of UVR on planktonic algal communities in the boreal lakes of northwestern Ontario. Our growth rate responses to UVR varied among sites and dates, but generally both UVA and UVB inhibited microalgal growth. Nearly all previous studies of UVR have examined the effects on instantaneous photosynthetic rates and/or short-term metabolic processes. However, in nutrient-limited systems, such as boreal lakes, uncoupling of photosynthesis and algal growth is likely common (Nalewajko and Schindler 1976, Sterner et al. 1997, Berman-Frank and Dubinsky 1999).

Our results showed that phytoplankton sensitivity to UVR decreased throughout the summer, despite higher or similar UVR flux later in the summer (Table 4.1 and Fig. 4.1). This change in sensitivity may be due to seasonal shifts in algal assemblages (Xenopoulos et al. 2000). Phytoplankton species can exhibit different sensitivities to UVR either through direct avoidance or by protective pigmentation and repair mechanisms (e.g. Gala and Giesy 1991, Xiong et al. 1996). Not only can different species vary in sensitivity but the same species can physiologically adjust to UVR and thus change its sensitivity through time. Changes in phytoplankton sensitivity would mean that in-lake effects of UVR could vary with season as well (Gala and Giesy 1991, Smith et al. 1998, Xenopoulos et al. 2000). Thus, phytoplankton should be more sensitive to UVB in spring than in summer or fall, because previous exposure of spring phytoplankton to UVR is minimal, due to ice and snow cover and generally low UVR flux.

Phytoplankton from L224 were generally more sensitive to UVR than phytoplankton from L302S, even late in the summer (Table 4.3). Phytoplankton can be protected from UVR in lake waters with high DOC that strongly attenuates UVR (West et al. 1999). Phytoplankton in L302S were exposed to lower UVR doses than in L224 (Table 4.1). Whether this can explain differences for L224 (low DOC lake) and L302S (higher DOC lake) is difficult to assess because L302S's algal taxonomic composition differed from L224's. The taxonomic composition of L302S changed from mainly chrysophytes to dinoflagellates following the artificial acidification of the lake (Findlay et al. 1999, Leavitt et al. 1999). Because transparency to UVR also increased (Donahue et al. 1998), this lake may already contain species adapted to high UVR, particularly



since the photoprotective pigment, scytonemin, has been recently found in the lake's sediments (Leavitt et al. 1999). Many other factors varied between our experiments, such as nutrient status of cells, temperature and algal densities. All of these factors potentially affect cellular physiology and/or growth rates for individual algal species under different light intensities and further complicate direct comparison of our results from the two study lakes.

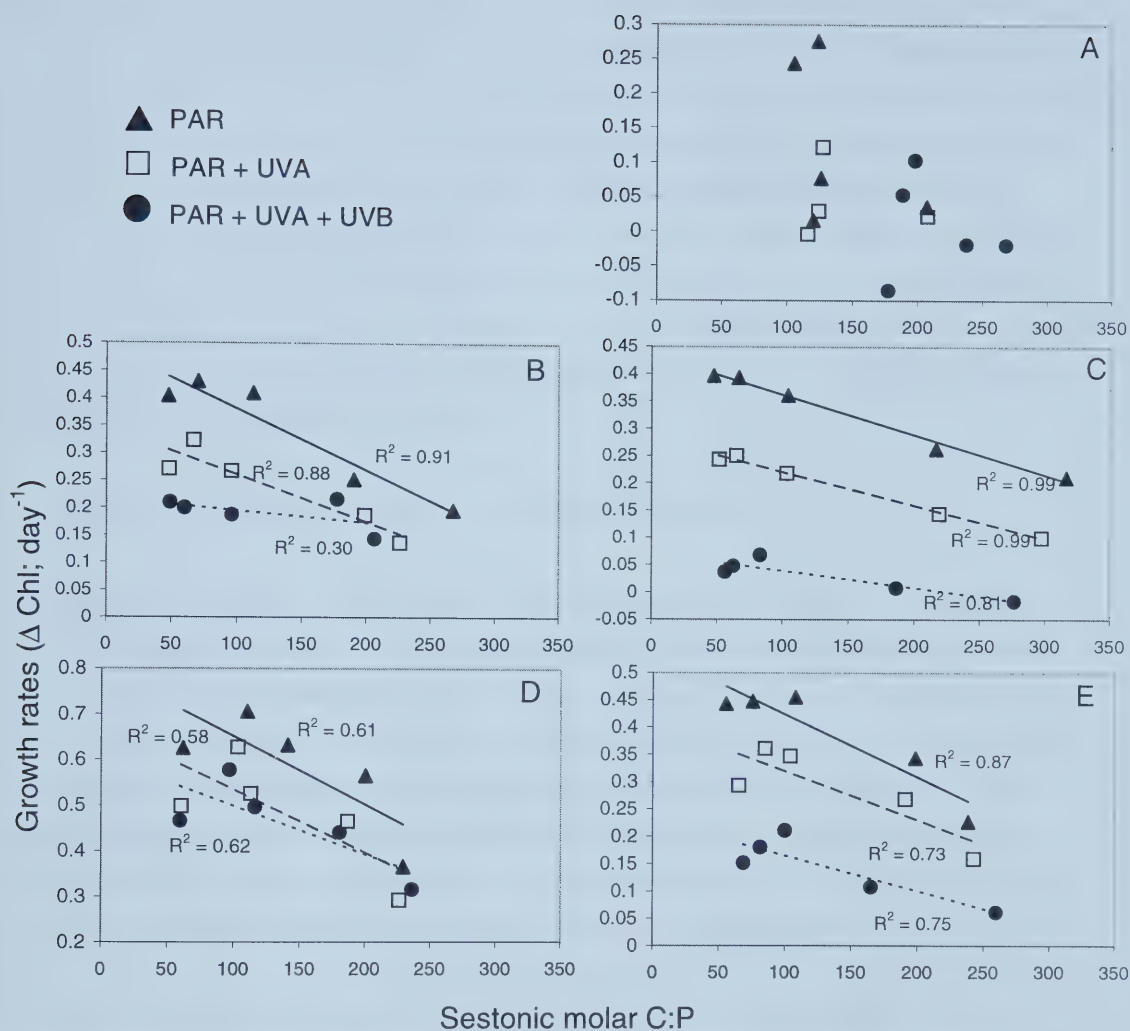
### **The effect of UVR on phytoplankton stoichiometry**

There are strong links between the growth rates and elemental composition of algae (Droop 1973, Goldman et al. 1979). For instance, low C:P ratios generally accompany higher rates of algal or vascular plant growth (Nielsen et al. 1996). Consistent with past findings in our experiments, seston C:P negatively associated with seston C and chlorophyll growth rates (Fig. 4.5). However, the specific aspects of this relationship depended upon the light quality (Fig. 4.5). Adding UVA and UVB shifted the growth-C:P relationship toward the x-axis (Fig. 4.5). Phytoplankton growing at a slower rate due to high UVR exposure have a lower C:P than phytoplankton growing at the same rate on PAR. These results demonstrate that using elemental ratios as quantitative index of algal growth can be misleading in some situations, because the same C:P ratio can correspond to different growth rates depending upon the wavelength distribution of light irradiating the phytoplankton community.

We show here that UVR generally reduced seston C:P ratios in boreal lakes, although the mechanisms for this have not been examined. One likely explanation is that UVR impaired photosynthetic C acquisition (reduced net photosynthesis), reducing C:P ratios. It is also possible that UVR increased the supply of nutrients to the phytoplankton either by photolysing lake dissolved organic matter and releasing its bioavailable nutrients (Wetzel et al. 1995) or indirectly, by affecting competitors for nutrients (Xenopoulos and Bird 1997). In the latter scenario, the bacterioplankton, which are generally superior competitors for P (Currie and Kalff 1984) are more sensitive to UVR than the phytoplankton (e.g. Jeffrey et al. 1996), providing the latter a competitive advantage. Both of these scenarios would decrease sestonic C:P ratios, as phosphorus would become relatively more abundant for algal uptake.

Finally, another possible explanation for the decrease in C:P is that UVA and UVB increased the need for nutrients to be used for repair. If, for example, cells increase RNA (a P-rich biomolecule) content to increase production of repair proteins, then algal C:P and N:P ratios





**Figure 4.5.** Variation in chlorophyll growth rate as a function of C:P ratios in three different light regimes for A to E, experiments 1 to 5 respectively. No significant linear relationships were found in A.





may decrease under enhanced UVR. Further studies are needed to determine which one (or combination) of these scenarios prevail in high UVR environments.

The C:Chl ratios in this study were widely variable, which complicates their use as surrogate measures of algal biomass. The cellular chlorophyll, phosphorus and carbon content are highly dependent on species, growth conditions and physiological state of the cell (Healey and Hendzel 1979). For example, phytoplankton cells are known to change their Chl content either following inhibitory light, shade adaptation, or even nutrient limitation (Healey and Hendzel 1979).

Responses to changing light and nutrient conditions can lead to transient dynamics in which C-fixation, cell division, and pigment synthesis (Chl) operate at different rates leading to variable C:Chl ratios. Our data show that an increase in C:Chl ratios can be caused by UVR. Thus, future studies considering the responses of plankton communities to UVR should interpret results that include only C or Chl changes with caution.

### **Co-regulation of phytoplankton growth by UVR and P supply?**

Our results show that the inhibition of growth by UVR appeared to interact with the availability of P. Reducing P-limitation or UVR alone did not greatly stimulate growth; only the removal of both led to substantially increased growth. In theory, a biological process can only be limited by one resource at a time (originating from Liebig's Law). However, there is increasing evidence of co-limitation by various factors in aquatic systems (e.g. Elser et al. 1990, Morel et al. 1994). Co-regulation by low nutrient (N and/or P) and high UVR may explain why alpine lakes generally have low densities of algae. Alpine lakes contain especially low DOC and receive higher incident UVR than low altitude lakes. Such ideas should be studied in future research.

The interaction between sunlight (PAR + UVR) and nutrients on algal growth, as shown here, is likely to be complex, because both light and nutrients are essential in sustaining ecosystem function (Urabe and Sterner 1996, Sterner et al. 1997). However, previous work has mostly considered the role of PAR quantity only (e.g. Urabe and Sterner 1996, Sterner et al. 1997) but in the water column there are both quantitative and qualitative changes in light with depth. Hence, plankton ecologists may need to pay particular attention to the UVR exposure of algal communities.



Here we show the interactive effects of UVR and P-limitation, two important stressors, on aquatic producers. We found that the negative effects of one stressor, UVR, were dependent, in part, on the absence/presence of another well known stressor, chronically low P concentrations. This supports previous work that showed that understanding the role of multiple stressors in ecosystems requires knowledge of both factors and their interactive effects (Schindler et al. 1996, Folt et al. 1999, Leavitt et al. 1999).

### **UVR effects on pelagic food webs**

UVR exposure generally lowered sestonic C:P ratios in our bioassays, which would improve the stoichiometric food quality for herbivores (Sterner et al. 1993, Elser et al. in press). This is contrary to what has been predicted or shown previously. UV exposure reduced P-uptake (Hessen et al. 1995) or increased carbohydrate storage (Van Donk and Hessen 1995) and resulted in increased algal C:P ratios. While it is generally assumed that direct UVB exposure will be detrimental to secondary and primary consumers (e.g. Williamson et al. 1997), in our case UVB could be indirectly beneficial for herbivores. However, whether UVR ultimately benefits organisms higher in the food web depends on total phytoplankton production and growth relative to the simultaneous 'improvement' in food quality.

The extent of UVR damage also depends on the rates of mixing (Neale et al. 1998) that control exposure of the phytoplankton to high UVR at the surface, and the mixing depth (Xenopoulos et al. 2000). Unfortunately, natural mixing is difficult to imitate in short-term bioassay experiments. Cells that live in a well-mixed layer can either benefit or become severely damaged from UVR exposure (see review by Roy 2000). Hence, it is difficult to compare our results to what happens under natural conditions without actually quantifying specific aspects of the kinetics of damage and repair (see review by Neale 2000). In our study, phytoplankton were held at a fixed depth throughout the growth bioassays, simulating phytoplankton trapped in near-surface waters for three days. The combination of sunny days and near-windless conditions can result in the formation of near-surface thermoclines (Imberger 1985). Such near-surface thermoclines occur with great frequency and are very common in boreal lakes (Xenopoulos and Schindler, in press see chapter 3). Nevertheless, the phytoplankton in this experiment were exposed to higher irradiances in the near-surface waters than if they were naturally mixing. Clearly more work is needed to determine the extent and duration of UVR exposure under field conditions and to



establish how this translates into altered growth and elemental composition such as we show here. Furthermore, potential ecological consequences higher in the food web also need to be evaluated.

### **UVR as an environmental factor in aquatic and terrestrial life**

Primary producers require sunlight for survival. Exposure to significant levels of UVB is a necessary consequence of obtaining PAR. In terrestrial plants, the most consistent observed response to high UVB is changed leaf concentrations of UVB absorbing or protective compounds (Day 2001). These compounds also act as antioxidants or chemical defenses against pathogens and herbivores and potentially change leaf elemental composition. High UVB exposure was found to increase foliar nitrogen concentration and decrease carbohydrates (Lindroth et al. 2000). In contrast, other plants increase their content of carbohydrate-rich secondary metabolites (tannins and lignin) under elevated UVB (Day, in press; Rozema et al. 1997). It is unclear, however, whether changes in leaf biochemistry translate into changes in tissue composition and what consequences altered plant C:N:P ratios would have on rates of litter decomposition and food quality for insect herbivores.

Regardless of likely future changes in UVR due to stratospheric ozone depletion (Xenopoulos and Schindler 2001) or drought and acid rain (which reduce DOC in lakes; Schindler et al. 1996), our results demonstrate that *ambient* levels of UVR can strongly affect algal growth and physiological condition. Although there is increasing evidence that UVR is an important factor influencing many biological processes in ecosystems, UVR has not yet been integrated into recent basic ecology (e.g. Begon et al. 1996, Dodson et al. 1998) or limnology text books (e.g. Lampert and Sommer 1997). Although modeling effects on aquatic ecosystems is a tedious task, ecosystem models should begin to consider the role of UVR in aquatic ecosystems. Ultimately, the effects of UVR depend on the stratification regime, the kinetics of UVR exposure (dose and dosage rate, e.g. Cullen and Lesser 1991) and repair (e.g. Neale 2000), and as we show here, interactions with other ecological factors such as nutrient supply.





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## 5. DIFFERENTIAL RESPONSES TO UVR FROM THE BACTERIO- AND PHYTOPLANKTON NEAR THE SURFACE AND BASE OF THE MIXED LAYER<sup>4</sup>

### INTRODUCTION

Epilimnetic waters in lakes are generally considered to have relatively even temperature distributions (Hutchinson 1957). However, when low wind speeds and intense solar radiation occur, near-surface, secondary or diurnal thermoclines can develop (Imberger 1985). Near-surface thermoclines with temperature differences as small as 0.02°C can restrict mixing and the layers can be as shallow as a few centimeters (Imberger 1985; Shay and Gregg 1986; Spigel and Imberger 1987; MacIntyre 1993). Although these near-surface thermoclines are important physical features in lakes (Imberger 1985; MacIntyre and Melack 1995), their ubiquity in nature and role in aquatic ecosystems remain underappreciated (Xenopoulos and Schindler, in press). They occur as frequently as one in every three days in large lakes (>60 ha) of the boreal forest and almost every day in smaller lakes (Xenopoulos and Schindler, in press). Once near-surface thermoclines are formed they generally persist for the rest of the day and are only eroded at night, usually by convective cooling (Brainerd and Gregg 1993, 1995). They can persist for several days, especially with light winds and warm air temperatures, in small protected lakes in forested areas. A study by Imboden et al. (1983) showed that an average of 75% of the day is characterized by the presence of secondary thermoclines in Lake Baldegg, Switzerland. In fact, strong winds ( $> 3.5 \text{ m s}^{-1}$  or  $> 12.6 \text{ km h}^{-1}$ ) were necessary to achieve complete mixing of the mixed layer.

This secondary stratification affects physico-chemical conditions that are important to phytoplankton (e.g. light exposure, nutrients and gases), and alter ecological processes mediated by resident organisms. For example, when isolated by secondary thermoclines, phytoplankton populations near the lake's surface experience greater irradiance and have different photoadaptive properties (cellular chlorophyll content, photosynthetic performance, etc.) compared to populations at the base of the mixed layer (Lewis et al. 1984a,b; Vincent 1990; Falkowski 1983; Neale et al. 1998a; Walsby 2001; Köhler 1997; Peña et al. 1990; Rodríguez et al. 2001).

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<sup>4</sup> A version of this chapter has been submitted for publication. Xenopoulos, M.A. and Schindler, D.W. *Freshwater Biology*.





Any organism trapped in the near-surface layer will have high exposure to ultraviolet radiation (UVR), which can affect their growth and physiological state (Vincent et al. 1984; Milot-Roy and Vincent 1994; Xenopoulos et al. 2000; Xenopoulos et al., in press). UVR can affect ecological processes very quickly. For instance, inhibition of photosynthesis occurred after just 15 minutes of UVR exposure while recovery required up to 24 hours (Gómez et al. 1998; Neale et al. 1998b). Interactions among layers, UVR exposure and changes in biological functions remain poorly studied and generally unclear (Neale et al. 1998a; Xenopoulos et al. 2000).

In this study, we addressed two questions: 1) does UVR affect phytoplankton and bacterioplankton trapped in near-surface waters? and 2) can populations from the bottom of the mixed layer physiologically adjust to a new high UVR environment if trapped near the surface by secondary stratification? To address these questions, we transplanted phytoplankton and bacterioplankton from the base of the mixed layer to near-surface waters and compared their responses to UVR to those simultaneously monitored in plankton collected from surface waters. Similar transplants have been used to study acclimation potential and sensitivity of benthic macroalgae to UVR (Larkum and Wood 1993; Karsten et al. 2001).

## METHODS

### **Site and lake description.**

Experiments were conducted in two small boreal lakes of the Experimental Lakes Area (ELA) in northwestern Ontario (49°40'N, 93°44'W) during the summer of 1999. Some physico-chemical parameters of the experimental lakes, Lake 224 (L224) and Lake 302S (L302S), are presented in Table 5.1.



**Table 5.1.** Some physico-chemical characteristics of the lakes that were sampled.

	224	302S
Z <sub>max</sub> (m)	27.4	10.6
A <sub>0</sub> (ha)	25.5	10.9
Thermocline (m)	~6 m	~5 m
K <sub>dPAR</sub> (m <sup>-1</sup> )	0.24	0.6
DOC (mg L <sup>-1</sup> )	3.2	4.2
1% UVB penetration (m)	1.5	0.75
Chlorophyll <i>a</i> (µg L <sup>-1</sup> )	0.5 – 1.5	0.8 – 2.0
TP (µg L <sup>-1</sup> )	4	8
Experimental manipulation	Reference	Eutrophication (1972-1975) Acidification (1981-1992)

### Experimental design.

Prior to beginning the experiment, a temperature profile was taken to determine the depth of the mixed layer. The bottom of the mixed layer was calculated as the shallowest point where the temperature change between it and the depth one meter below was greater or equal to 1°C. Experiments began mid-morning (~10:30-11 a.m.) on calm (wind <5 km h<sup>-1</sup>) days when a distinct temperature difference (>0.4°C) was found between the surface and base of the mixed layer.

Water samples were taken from the surface (first 25 cm; hereafter called surface samples) and ~30 cm above the bottom of the mixed layer (hereafter called base samples) with a peristaltic pump. Base samples were carefully pumped to prevent contamination with metalimnetic waters. Two-liter subsamples of surface and base water were saved for laboratory analysis. Depths of the base samples are presented in Table 5.2. One-liter aliquots of surface and base water were placed in 1.2 L Whirlpak polyethylene bags (NASCO plastics, Burlington, Ontario, Canada). The bags



were placed inside floating wire-baskets at a depth of 30 cm. The bags are transparent to solar radiation (Cockell and Rothschild 1999).

Three solar radiation treatments (from here on called UVR treatments) were produced with the use of plastics sheets (Cadillac Plastics, Winnipeg, Manitoba, Canada) designed to block different wavelengths. The treatments were:

- 1) PAR + UVA + UVB (OP-4, 50% cutoff = 280 nm),
- 2) PAR + UVA (Mylar-D, 50% cutoff = 318 nm) and
- 3) PAR only (OP-3, 50% cutoff = 400 nm).

Two bags from each treatment and depth were removed after 4, 24 and 48 hours and processed as described below. The experiments were carried out three times in each lake (Table 5.2).

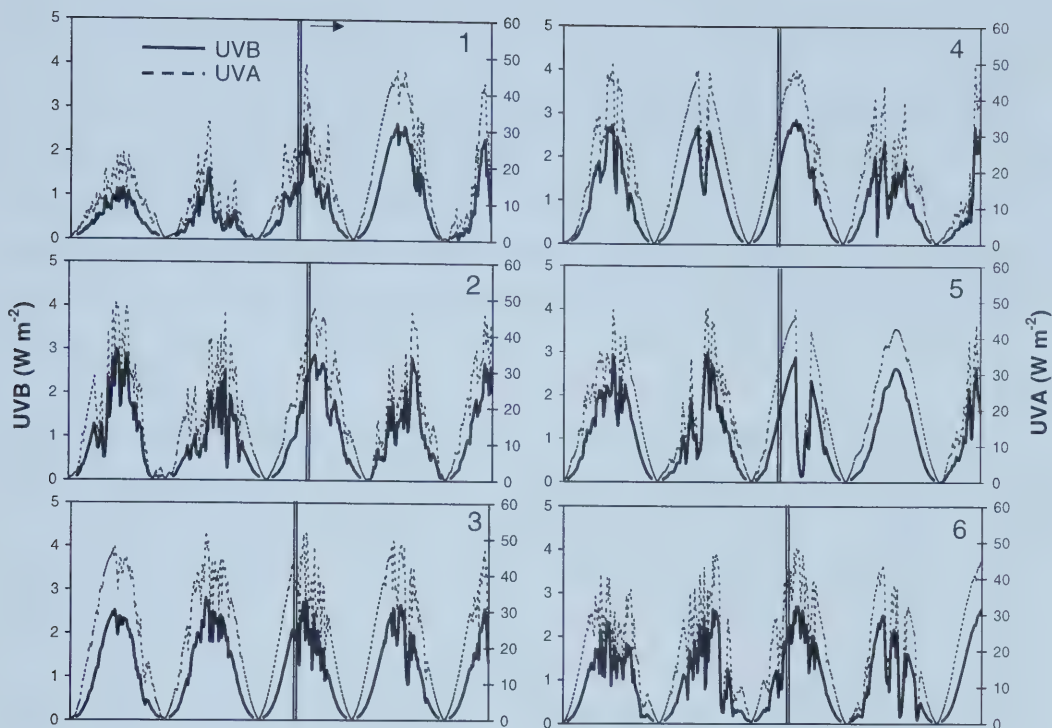
**Table 5.2.** Experiment number, lake, dates and depth of the initial ‘base’ sample for each of the experiments.

Exp. #	Lake	Dates (in 1999)	Depth (m)
1	302S	2-4 June	2.8
2	224	8-10 June	3.5
3	302S	17-19 June	3.0
4	224	11-13 July	4.0
5	302S	23-25 July	2.8
6	224	4-6 August	4.0

### Solar radiation measurements.

Incident surface UVA and UVB were measured at 10-minute intervals with wide-band UVA (320-400 nm) and UVB (280-320 nm) sensors (BW20 Vital Technologies) attached to a Li-Cor data logger (output in Volts) and cross-calibrated with a Li-Cor Model LI-1800UM Spectroradiometer (output in  $\text{W m}^{-2}$ ). Daily surface PAR was measured at 1-second intervals using a Li-Cor quantum sensor and recorded for a 10-min average. Surface UVR and PAR measurements were made at the ELA meteorological station located ~2.5 km from the lakes. UVA and UVB dose rates throughout the six experiments and two days prior are shown in Fig. 5.1.





**Figure 5.1.** Surface UVB (solid line) and UVA (dashed line) dose rates for experiments 1 to 6 during the incubation and two days prior to the beginning of the experiment. The double line indicates the start of the experiment.





## **Chlorophyll *a* and Phytoplankton Production.**

Chlorophyll *a* (chl *a*) was extracted in boiling ethanol and determined fluorometrically (Nusch 1980). Primary production samples were incubated in a growth chamber (Shearer and Fee 1974) no longer than ~1h to avoid photoadaptation or repair of DNA-damage by phytoplankton. In general, the rate of recovery is slower than the rate of depression and a 60-minute incubation probably was not long enough for full recovery to occur (Buma et al. 1995; Neale and Richerson 1987).

Samples were inoculated with 20  $\mu\text{Ci mL}^{-1}$  of  $\text{NaH}^{14}\text{CO}_3$  and incubated at the ambient lake temperature. Samples were exposed to PAR levels of 300-500  $\mu\text{Ein m}^{-2} \text{s}^{-1}$ , depending on the lake and experiment, which is roughly 30% less than what they were exposed to in the lake (at 25 cm) during solar noon. The lamp (GE Lucalox, High pressure sodium lamps, 150W) emitted no UVB radiation or short-wave UVA radiation. At all times the samples were exposed to saturating light levels (but not photoinhibiting) as determined from photosynthesis-irradiance curves in pilot studies in the summer of 1998 (unpublished data). After incubation, residual inorganic carbon was driven off by the addition of 250  $\mu\text{L}$  of 6N HCl followed by air bubbling for 20 min. Incorporation of  $^{14}\text{C}$  into phytoplankton was determined by liquid scintillation counting. Photosynthesis rates were calculated from dissolved inorganic concentrations (DIC) after dark correction. Measurements of DIC were made using infrared detection of  $\text{CO}_2$  (LIRA infrared analyzer model 202). Rates of  $^{14}\text{C}$  uptake were determined after 4 and 48-hour incubations.

## **Respiratory-enzyme activity**

The ETS (electron transport system) assay was used to measure plankton respiration as in Rai (1984) and del Giorgio (1992). ETS-activity is measured as the rate of INT (2-p-Iodophenyl-3-p-nitrophenyl-5-phenyl-tetrazolium Chloride) reduction, which is then converted to equivalent oxygen. Reagents were prepared as in Rai (1984). Samples (300 mL for L224 and 150 mL for L302S ) were filtered on 0.4  $\mu\text{m}$  polycarbonate membrane filters under low vacuum. The filters were placed in plastic 7 mL tubes with 2 mL of homogenation buffer and kept at 4°C prior to sonicating for 5 min. A 1 mL aliquot was taken from the cell homogenate and placed in a centrifuge tube with 3 mL substrate buffer and 1 mL INT solution and incubated for 10 min at the lake temperature. The reaction was stopped by adding 1 mL of termination solution. The reduced



INT solution in the centrifuge tubes was clarified by centrifugation (15 min at 5000 rpm) and the absorbance of an aliquot was read in a spectrophotometer at 490 nm. Microplankton respiration rates were calculated from the ETS activity as by the equation in Rai (1984). Respiration rates were determined after 4 and 48-hour incubations.

### Bacterioplankton production

Bacterial production was determined by protein synthesis rates as described in Smith and Azam (1992). An aliquot of 1.5 mL from each treatment was added to a sterile 2.0 mL microcentrifuge tube to which 5  $\mu$ L of L-[4,5- $^3$ H] Leucine (specific activity, 40-60 Ci mmol $^{-1}$ ) was added.

Trichloroacetic acid (TCA, 90 $\mu$ L of 100% (w/v)) was added to blank tubes. All tubes were incubated at lake temperature for ~45 min in a growth chamber. Incubations were in the dark to avoid destruction of the radiolabeled leucine in the light (Jeffrey et al. 2000). Samples were run with 3 replicates and 2 blanks. Incubations were terminated by the addition of TCA (5% final concentration). The tubes were centrifuged for 10 minutes at 16 000 X g and aspirated. The aliquots were washed by the addition of 1.5 mL of 5% TCA and mixed. Samples were centrifuged again for 10 min and aspirated. Liquid scintillation cocktail was added directly to the microcentrifuge tube and mixed. Incorporation of  $^3$ H-Leucine by bacteria was assayed in a liquid scintillation counter. Bacterial carbon production rates were calculated by using a carbon: protein conversion factor of 0.86 (Smith and Azam 1992). Bacterioplankton production rates were determined after 4 and 48-hour incubations.

### Stratification and UVR exposure

We defined an index of previous UVR exposure (UVPE) which takes into account the UVA and UVB at the surface of the lake (J m $^{-2}$ ) and a stratification parameter PE (J m $^{-2}$ ) as:

$$UVPE = UVR * PE, \quad (1)$$

where UVR is the sum of UVB and UVA (J m $^{-2}$ ), and PE (J m $^{-2}$ ) is equivalent to the amount of energy required to vertically homogenize the water layer (Nelson et al. 1989). PE is defined by:

$$PE = (1/12) \Delta\rho \cdot g \cdot z^2, \quad (2)$$

where g (m s $^{-2}$ ) is the acceleration due to gravity,  $\Delta\rho$ (kg m $^{-3}$ ) is the density gradient between the surface and bottom of the mixed layer ( $\rho_{\text{bottom}} - \rho_{\text{surface}}$ ) and z (m) is the depth of the mixed layer. A high PE number would indicate very stable stratification and the presence of near-surface thermoclines (low mixing).



We found the product (as opposed to the sum) of PE and UVR to give a more accurate description of the light/stratification history because of the importance of intermediate UVR and PE values. Hence, two values of opposite extremes (i.e. high PE but low UVR) are weighted less than two intermediate values (intermediate UVR and PE). Two high values (high UVR and low mixing conditions or high PE) yield the maximum number. Data for the index were collected for the two days prior to the commencement of the experiment.

### Statistical Analysis

Initial surface and base samples were compared with a two-tailed, student t-test ( $P = 0.05$ ) after testing for homoscedascity. Preliminary results indicated that initial (time=0) surface and base samples were often significantly different. Hence, base and surface samples were evaluated separately with a one-way analysis of variance for the effects of UVR treatment for each time period sampled (4, 24 and 48 hours or 4 and 48 hours where applicable) on production and respiration rates, and cellular chlorophyll. Differences between UVR treatments were further assessed with Tukey-Kramer multiple comparison tests. All significant results are reported at the 0.05 level. Photosynthetic (P) and respiration (R) rates were also assessed per unit of chl *a* (B). Standard errors of the ratios (P/B and R/B) and chlorophyll growth (calculated as percent change from initial sample) were calculated from the sum of the squared coefficient of variations of the means as in Colquhoun (1971). Significant differences between ratios (P/B and R/B and chl growth) were assessed using their respective 95% confidence limits (calculated using the critical t value).

## RESULTS

### Comparison of surface and base samples at time 0

Chl *a* concentrations in water samples from the base of the epilimnion were always significantly higher than those taken from the surface at the start of the experiments (t-test results, Table 5.3). Conversely, carbon-fixation rates were significantly higher in the surface algal populations at the start of experiments 1 and 4 and not significantly different in the remaining experiments (Table 5.3). Chlorophyll-specific photosynthesis (P/B), was higher in surface populations of experiments 1, 3 and 4 (Table 5.3). Initial bacterial production rates were not significantly different between





depths except in experiment 6, where they were higher at the surface (Table 5.3). Planktonic ( $>0.4 \mu\text{m}$  fraction) respiration rates were significantly higher in surface samples than in base samples at the start of experiments 3 and 4 (Table 5.3).

### **UVR effects on surface phytoplankton growth**

In experiments 1 (L302S) and 4 (L224) surface algae had reduced growth (% change in chl *a* from initial sample) in all treatments throughout the incubation period (Fig. 5.2). Comparisons of confidence intervals showed that UVR treatment did not affect surface phytoplankton growth except in Experiment 3 after 48-hour exposure, where growth was significantly higher in the PAR only treatment (Fig. 5.2).

### **UVR effects on base phytoplankton growth**

All wavelengths of solar radiation negatively affected growth in base algae, even after 48 hours (Fig. 5.2). In most experiments, transplantation to high solar exposure caused reduced growth in base algae. Comparisons of confidence intervals showed that UVR treatment did not affect base phytoplankton growth (Fig. 5.2).

### **UVR effects on surface chlorophyll**

Exposure to UVA and UVB did not affect chl *a* concentrations in surface samples except in experiment 1 (L302S), after a 4-hour exposure (Table 5.4). In that experiment, treatments exposed to UVB and UVA had 30% less chlorophyll than the PAR only treatment (not shown).

### **UVR effects on base chlorophyll**

In the base populations, UVR treatments inhibited chl *a* only in experiment 1 (L302S), 2 (L224) and 4 (L224) after 48h exposure and in experiment 5 (L302S) after 4h exposure (Table 5.4). Multiple comparison tests showed that base samples from experiment 1 exposed to PAR+UVA+UVB and PAR+UVA were 30% lower than samples exposed to PAR only (not shown). In experiment 2, samples exposed to PAR+UVA and PAR+UVA+UVB had 25% less chlorophyll than the samples exposed to PAR only. In experiment 4, chl *a* was 55% lower in base samples exposed to PAR+UVA+UVB and PAR+UVA than those exposed to PAR (not shown).





Finally, in experiment 5, base samples exposed to PAR+UVA+UVB had 31% less chlorophyll than samples exposed to PAR+UVA and PAR only after 4 hours (not shown).

### **UVR effects on surface primary production**

Photosynthetic rates of surface algal populations were inhibited by UVR treatment only in experiment 4 (L224) after 48h exposure (Table 5.5, Fig. 5.3). In that experiment, photosynthesis was ~50% lower in samples exposed to PAR+UVA+UVB compared to the other 2 treatments (Fig. 5.3). Exposure to PAR+UVA and PAR+UVA+UVB did not affect photosynthesis per unit biomass (P/B) in surface samples (Fig. 5.3).

### **UVR effects on base primary production.**

UVR reduced the photosynthetic rates of the base populations only from experiments 1 after 4h and 48h exposures, in experiment 4 after 48h exposure and in experiment 5 after 4h exposure (Table 5.5). In those experiments, PAR+UVA caused a reduction in photosynthetic rates of 50 to 85% compared to the PAR only treatment (Fig. 5.3). PAR+UVA+UVB caused an additional reduction in photosynthesis of ~25% in experiment 1 (Fig. 5.3) compared to the PAR only treatment. P/B was significantly lower in samples exposed to PAR+UVA and PAR+UVA+UVB in the base populations of experiment 1 (L302S) after 4-hour exposure and experiment 4 (L224) after 48-hour exposure (Fig. 5.3).

### **UVR effects on surface bacterial production.**

UVR treatment affected surface bacterioplankton production in all three experiments (2, 5 and 6) after 4 and 48h exposures (Table 5.6, Fig. 5.4). After 4-hour exposure, bacterial production was generally 25%-68% higher in treatments that excluded UVA and UVB (Fig. 5.4). However, the opposite was found after 48-hour exposure; bacterial production was generally lower in treatments that excluded UVA and UVB (Fig. 5.4).



**Table 5.3.** Absolute *t* values and associated probability (*P*) comparing initial samples (time = 0) from the surface to those from the base of the mixed layer. Statistical significance of chl *a*, photosynthesis rates (*P*), specific photosynthesis (*P/B*), bacterioplankton production (*BP*), respiration rates (*R*) and respiration per unit chl *a* (*R/B*) were determined using two-tailed student *t*-test for experiments 1 to 6 as in Table 5.2. Where significant differences were found, the sign in parenthesis indicates if the surface sample was higher (+) or lower (-) than the base sample.

#	Chl <i>a</i>	<i>P</i>	<i>P/B</i>	<i>BP</i> <sup>†</sup>	<i>R</i>	<i>R/B</i>
1	7.57* (-)	7.33* (+)	6.95* (+)	Nd	Nd	Nd
2	4.30* (-)	0.59 <sup>NS</sup>	0.90 <sup>NS</sup>	1.80 <sup>NS</sup>	Nd	Nd
3	38.63*** (-)	0.33 <sup>NS</sup>	3.14* (+)	Nd	5.89* (+)	8.81** (+)
4	4.72* (-)	5.29* (+)	15.99** (+)	Nd	4.71* (+)	2.28 <sup>NS</sup>
5	4.71* (-)	1.01 <sup>NS</sup>	2.79 <sup>NS</sup>	1.92 <sup>NS</sup>	3.10 <sup>NS</sup>	3.49* (+)
6	10.39** (-)	Nd	Nd	3.15* (+)	1.08 <sup>NS</sup>	0.66 <sup>NS</sup>

Note:

Nd = Not determined.

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

NS = not significant.



**Table 5.4.** One-way ANOVA of the influence of UVR treatment (PAR+UVA+UVB, PAR+UVA and PAR only) on the chl *a* concentration from the surface and base of the mixed layer for each time (4, 24, 48 hours) sampled for experiments 1 to 6. Highlighted in bold are instances where UVR treatment was found to be significant ( $P < 0.05$ ). Where the UVR treatment was found to significantly affect chl *a*, Tukey-Kramer multiple comparisons test was used to determine further significance between UVR treatments. Different letters indicate treatments which differed significantly.

#	Time	Surface		Base	
		F	P	F	P
1	4h	<b>23.4</b>	<b>0.015</b>	0.7	0.580
	PAR+UVA+UVB		<b>a</b>		
	PAR+UVA		<b>a</b>		
	PAR only		<b>b</b>		
	24h	1.3	0.398	8.8	0.056
	48h	4.5	0.075	<b>28.6</b>	<b>0.011</b>
	PAR+UVA+UVB				<b>a</b>
	PAR+UVA				<b>a</b>
	PAR only				<b>b</b>
2	4h	2.7	0.213	4.6	0.121
	24h	6.0	0.089	6.4	0.083
	48h	0.6	0.607	<b>237.9</b>	<b>0.046</b>
	PAR+UVA+UVB				<b>a</b>
	PAR+UVA				<b>a</b>
	PAR only				<b>b</b>
3	4h	0.1	0.900	0.6	0.586
	24h	6.5	0.092	1.8	0.305
	48h	2.5	0.227	1.6	0.345
4	4h	0.1	0.890	4.3	0.131
	24h	0.01	0.995	0.4	0.715
	48h	1.0	0.476	<b>17.4</b>	<b>0.039</b>
	PAR+UVA+UVB				<b>a</b>
	PAR+UVA				<b>a</b>
	PAR only				<b>b</b>
5	4h	1.1	0.444	<b>36.7</b>	<b>0.0078</b>
	PAR+UVA+UVB				<b>a</b>
	PAR+UVA				<b>b</b>
	PAR only				<b>b</b>
	24h	0.5	0.657	1.5	0.347
	48h	0.5	0.656	4.0	0.144
6	4h	0.9	0.488	0.2	0.869
	24h	4.6	0.122	0.2	0.837
	48h	3.5	0.167	0.7	0.589

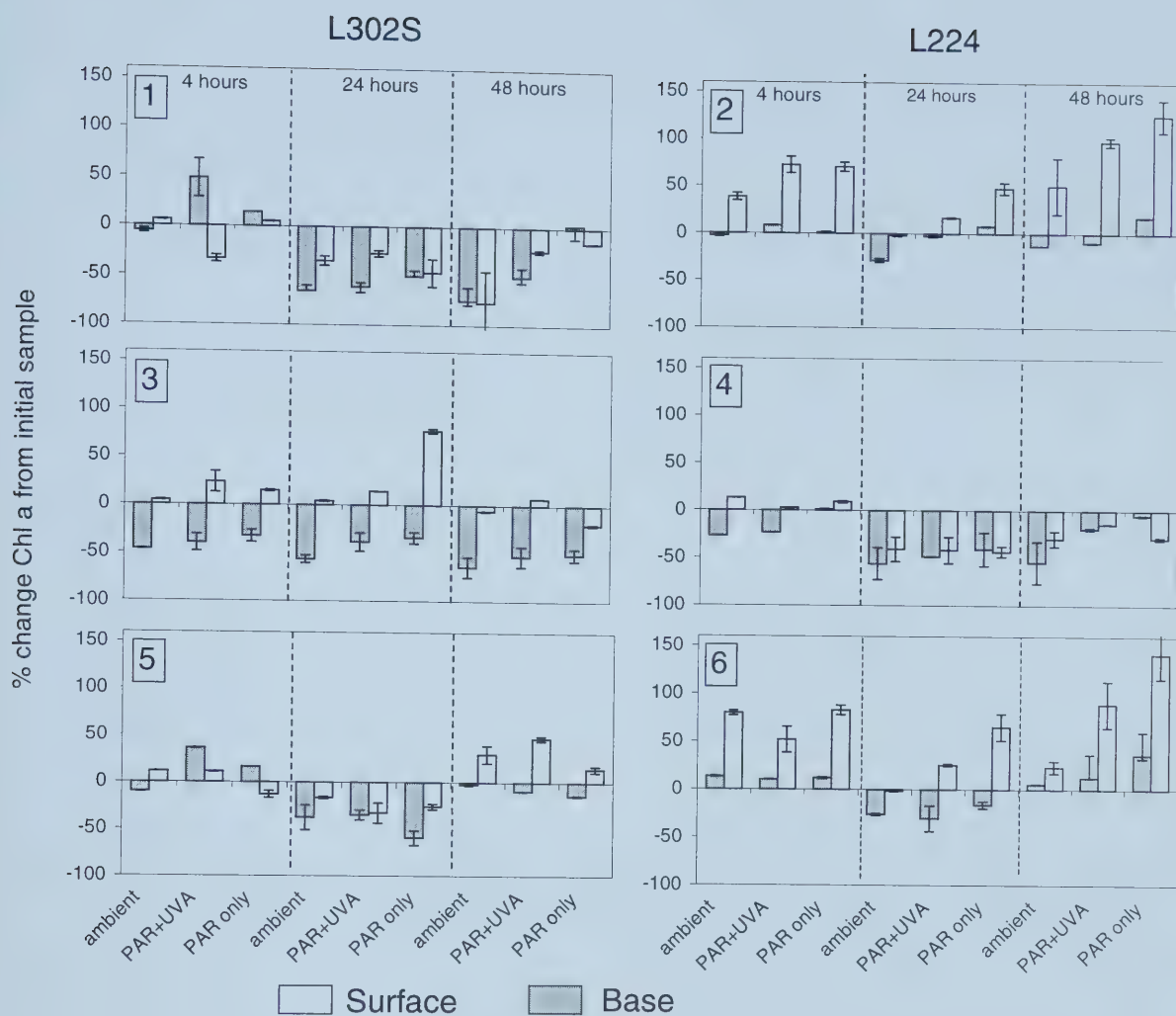


**Table 5.5.** One-way ANOVA of the influence of UVR treatment (PAR+UVA+UVB, PAR+UVA and PAR only) on photosynthetic rates from the surface and base of the mixed layer for each time (4, 48 hours) sampled for experiments 1 to 6 as in Table 5.2. Highlighted in bold are instances where UVR treatment was found to be significant ( $P < 0.05$ ). Further significance between UVR treatments was assessed using Tukey-Kramer multiple comparison test illustrated in Fig. 5.3.

#	Time	Surface		Base	
		F	P	F	P
1	4h	0.1	0.892	<b>63.1</b>	<b>0.004</b>
	48h	6.4	0.083	<b>15.0</b>	<b>0.027</b>
2	4h	5.5	0.099	0.04	0.966
	48h	4.7	0.118	4.2	0.134
3	4h	2.4	0.236	1.4	0.382
	48h	5.2	0.106	2.0	0.280
4	4h	0.7	0.547	5.1	0.109
	48h	<b>13.1</b>	<b>0.0331</b>	<b>409.5</b>	<b>0.0002</b>
5	4h	1.2	0.404	<b>25.0</b>	<b>0.013</b>
	48h	3.4	0.171	4.0	0.144
6	Not Determined				







**Figure 5.2.** Chl *a* growth in near-surface (clear bars) and base phytoplankton (dark bars) calculated as percent chl *a* change from initial sample for experiments 1 to 6. Error bars are standard deviations.

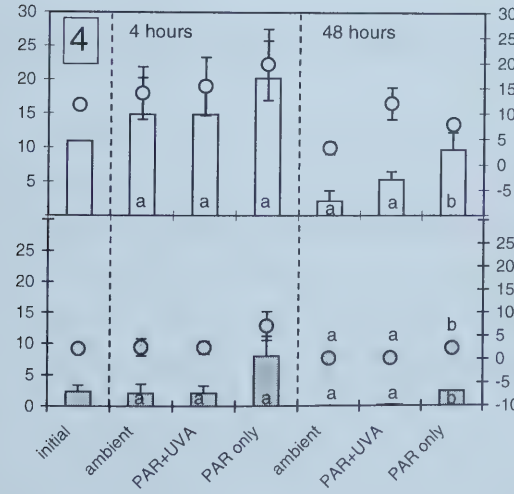
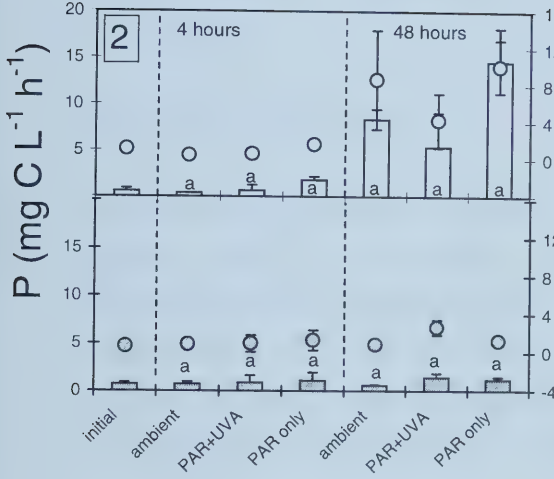




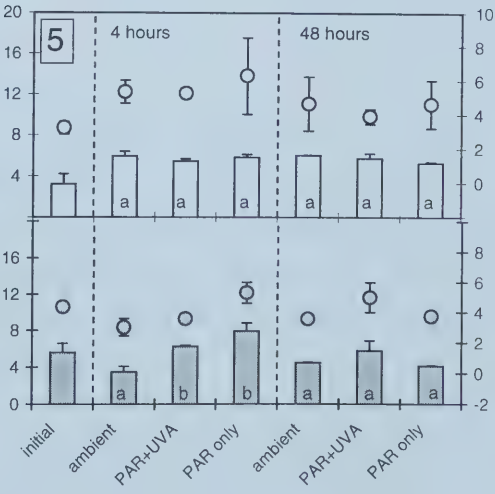
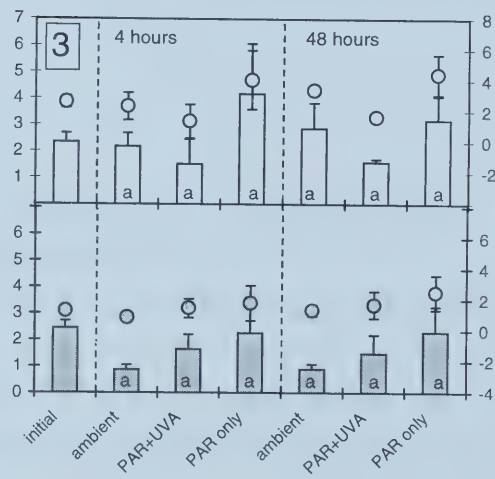
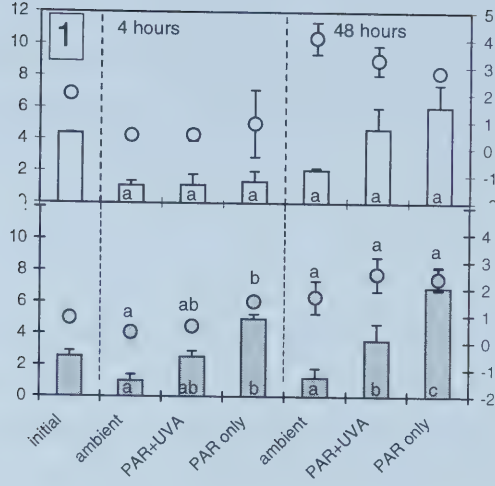
**Figure 5.3.** Photosynthetic rates (P, bars) and biomass-specific photosynthesis (P/B, circles) measured after 4 and 48-hour incubations in three UVR treatments for experiments 1 to 5 shown in boxes in upper left corner. Error bars are standard deviations. Different letters indicate UVR treatments that differed significantly ( $P < 0.05$ ) within one incubation period for photosynthetic rates (Tukey-Kramer HSD Test). Chl-specific photosynthesis was compared using 95% confidence intervals. Different letters indicate significant differences where found.

Base  
Surface

L224



L302S



P/B (mg C  $\mu$ g Chl a<sup>-1</sup> L<sup>-1</sup> h<sup>-1</sup>)



## **UVR effects on base bacterial production**

UVR treatment decreased bacterioplankton production rates in experiment 2 after 4h exposure and increased rates in experiment 5 after 48h exposure (Table 5.6, Fig. 5.4). No other significant differences were found.

## **UVR effect on surface respiration.**

UVR treatment affected surface respiration rates in experiment 3 (L302S) after 4h exposure only (Table 5.7). In experiment 3, samples exposed to UVB+UVA+PAR and UVA+PAR increased their respiration rates by ~45% compared to samples exposed to PAR only. Biomass-specific respiration rates (respiration per unit chl *a*, R/B) were variable and no effects of UVR were found (data not shown).

## **UVR effect on base respiration**

UVR treatment affected respiration rates only in the base samples of experiment 4 after 4h and 48 h exposure (Table 5.7). In experiment 4, respiration rates of base plankton, after 4 hours, were 40% higher in the UVA+PAR treatment and 50% higher in the UVB+UVA+PAR exposed than with PAR only treatments (not shown). After 48 hours, respiration rates of base plankton were ~80% higher in samples exposed to PAR+UVA+UVB and PAR+UVA compared to samples exposed to PAR only (not shown). R/B was not significantly different in the base experiments.

## **Stratification history and previous UVB exposure**

The lowest UVPE values are for experiments 1, 4 and 6 (Fig. 5.5). In experiment 1 and 6 both UVB flux (shown in Fig. 5.1) and water column stability were low prior to the beginning of our experiment, which means that algae were well-mixed and exposed to low UVB. In experiment 4, UVB was high two days prior to the experiment but the algae were well mixed. The highest values of UVPE were for experiments 2 and 5 (Fig. 5.5). These values were mainly associated with high UVB flux and stable stratification conditions.





**Table 5.6.** One-way ANOVA of the influence of UVR treatment (full sunlight, PAR + UVA and PAR only) and time (4, 48 hours) on the bacterioplankton protein synthesis rates from the surface and base of the mixed layer for experiments 2, 5 and 6. Highlighted in bold are instances where UVR treatment was found to be significant ( $P < 0.05$ ). Further significance between UVR treatments was assessed using Tukey-Kramer multiple comparison test shown in Fig. 5.4.

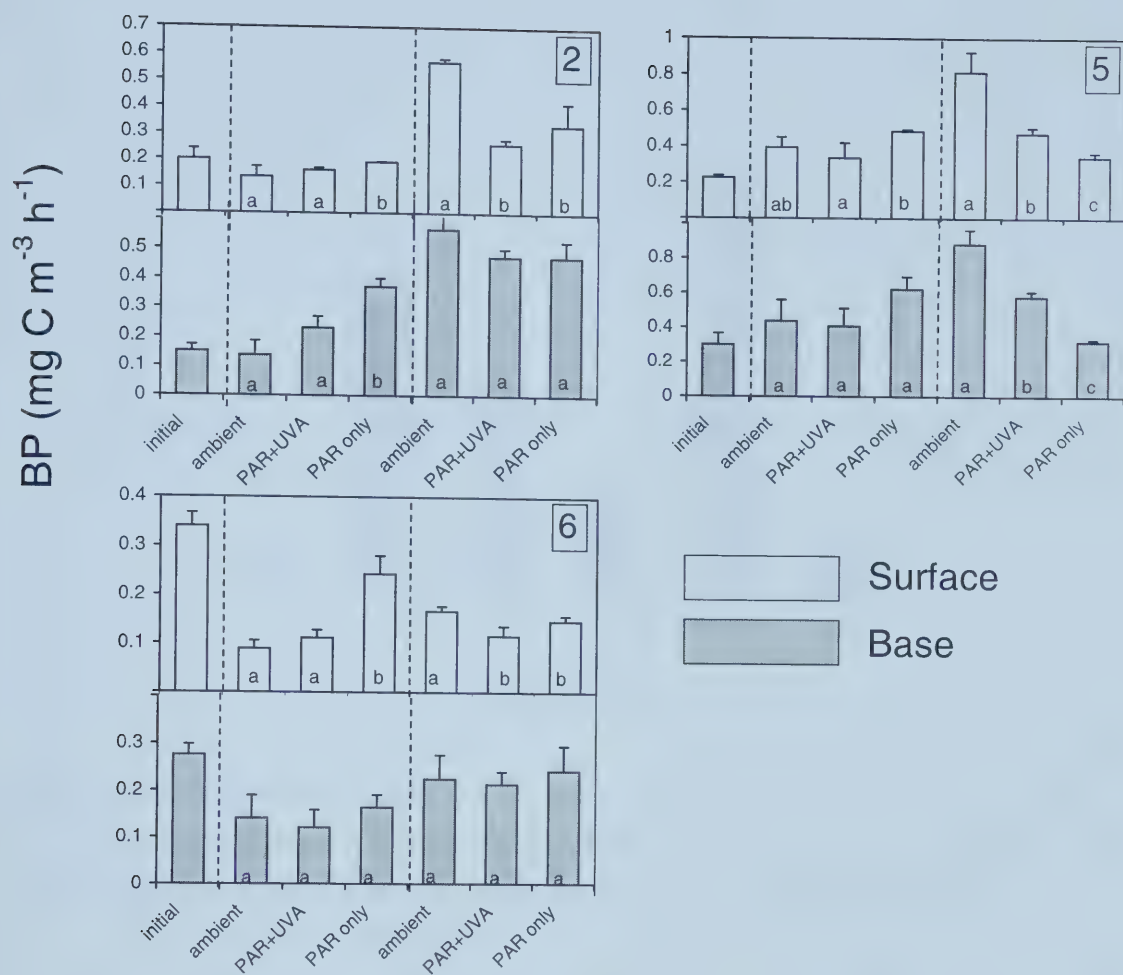
#	Source	Surface		Base	
		F	P	F	P
1	Not determined				
2	4h	<b>20.1</b>	<b>0.029</b>	<b>28.8</b>	<b>0.011</b>
	48h	<b>20.5</b>	<b>0.018</b>	0.6	0.621
3	Not determined				
4	Not determined				
5	4h	<b>5.1</b>	<b>0.048</b>	4.0	0.080
	48h	<b>39.1</b>	<b>0.0004</b>	<b>89.2</b>	<b>&lt;0.0001</b>
6	4h	<b>32.1</b>	<b>0.0006</b>	0.9	0.445
	48h	<b>6.6</b>	<b>0.031</b>	0.07	0.934



**Table 5.7.** One-way ANOVA of the influence of UVR treatment (PAR+UVA+UVB, PAR+UVA and PAR only) for the two time periods of exposure (4, 48 hours) on the plankton respiration rates from the surface and base of the mixed layer for experiments 3 to 6. Highlighted in bold are instances where UVR treatment was found to be significant ( $P < 0.05$ ). Where the UVR treatment was found to be significant, Tukey-Kramer multiple comparisons test was used to determine further significance between UVR treatments. Different letters indicate treatments which differed significantly.

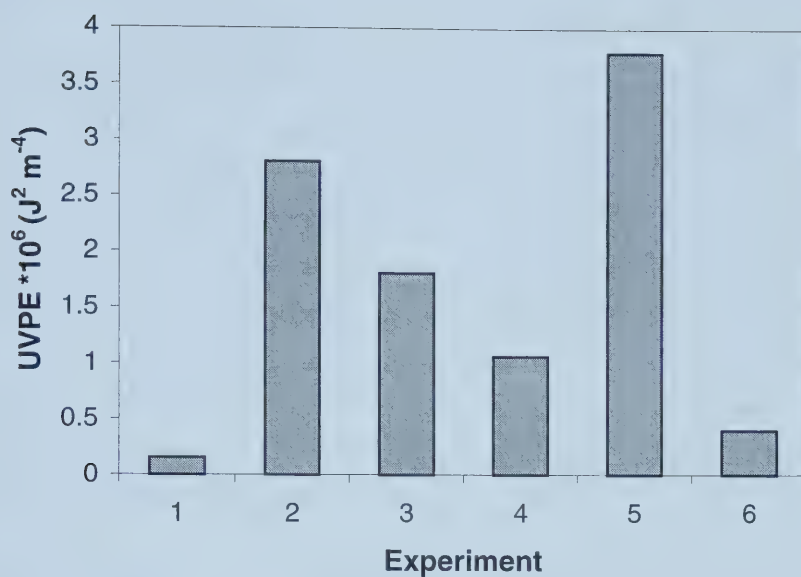
#	Time	Surface		Base	
		F	P	F	P
1	Not determined				
2	Not determined				
3	4h	<b>82.3</b>	<b>0.0024</b>	1.1	0.439
	PAR+UVA+UVB		<b>a</b>		
	PAR+UVA		<b>a</b>		
	PAR only		<b>b</b>		
	48h	1.1	0.450	5.3	0.103
4	4h	1.8	0.313	<b>47.2</b>	<b>0.0054</b>
	PAR+UVA+UVB				<b>a</b>
	PAR+UVA				<b>b</b>
	PAR only				<b>c</b>
	48h	1.2	0.423	<b>14.2</b>	<b>0.0294</b>
	PAR+UVA+UVB				<b>a</b>
	PAR+UVA				<b>a</b>
	PAR only				<b>b</b>
5	4h	1.0	0.475	7.9	0.0778
	48h	6.1	0.080	1.4	0.369
6	4h	0.9	0.497	4.6	0.124
	48h	1.3	0.399	0.8	0.528





**Figure 5.4.** Bacterioplankton production (protein synthesis rates) measured after 4 and 48-hour incubations in three UVR treatments for experiments 2, 5 and 6. Error bars are standard deviations. Different letters indicate UVR treatments that differed significantly ( $P < 0.05$ ) within one incubation period (Tukey-Kramer HSD test).





**Figure 5.5.** UVPE values for experiments 1 to 6. Values are two-day averages (2 days prior to the commencement of experiment). A high UVPE value indicates that the plankton were exposed to high irradiances under low mixing conditions prior to the commencement of the experiment.





## DISCUSSION

### Inter-lake comparison

We found that algae from the base of the mixed layer ‘trapped’ in shallow incubations are more sensitive to UVR than algae that originate from near the surface. Surface and base phytoplankton from L224 (high UVR penetration) and L302S (lower UVR penetration) showed similar responses when exposed to near-surface UVR. The strongest UVR effects were seen in experiments 1 (L302S) and 4 (L224). However, photoinhibition of photosynthesis was most commonly found in the base populations of L302S (a higher DOC lake, right side panels on fig. 5.3). In a previous study by Xenopoulos et al. (in press), the growth rates of phytoplankton *from the surface* of L302S were less affected by UVA and UVB exposure than those of L224. In this study, the base populations of the darker L302S are probably not accustomed to high levels of irradiance because they reside well below the 1% UVR zone.

### The effects of UVR and shallow stratification on phytoplankton

We found few effects of UVA and no effects of UVB on chl *a* or photosynthesis in phytoplankton that originated from near-surface waters, suggesting that photoadaptation or light acclimation are important factors minimizing UVR effects in surface waters. On the other hand, base algal populations grew slower and, in some cases, exhibited chl loss and photoinhibition when exposed to UVA and UVB. In most cases, base phytoplankton did not appear to acclimate to high light even after 48 hours of exposure and a longer period of adjustment to non-inhibited values is likely necessary, if the algae adjust at all.

Photoinhibition was not always found in the base phytoplankton incubated at shallower depths (i.e. experiments 2 and 3) and chl-specific photosynthesis generally remained unchanged after UVA and UVB exposure. Since UVR flux was not low during those experiments (Fig. 5.1), other factors (e.g. resilient algal assemblages, not measured in this study) may explain this discrepancy. We also found the time scales of responses to UVR to be variable. Sensitivity to UVA and/or UVB exposure was often not apparent until after a 48-hour exposure although, occasionally, only a 4-hour exposure to UVA and/or UVB was enough to cause damage with recovery being observed prior to the termination of the experiment. We suggest that this variability also reflects



the patchy time scales of the kinetics of damage and repair (e.g. Vincent and Neale 2000; Neale 2000). Damage and repair processes are dependent on the species composition and the interaction with other variables (for example, temperature: Roos and Vincent 1998 or nutrients: Xenopoulos et al. in press) that varied between our experiments.

Respiration rates were changed after UVR exposure only in two experiments. Respiration rates were not related to production rates in this study. Some past studies have found respiration not to be affected by UVR (Agulera et al. 1999; Larkum and Wood 1993; Watkins et al. in press), while others have found it to increase with UVR exposure (Ferreira et al. 1997).

### **The effects of UVR on bacterioplankton.**

Bacterioplankton from the surface waters were more negatively affected by UVA and UVB exposure than the bacterioplankton from the base after four hours of exposure (Fig. 5.4). However, exposure to UVA and especially UVB, increased bacterial production in the surface waters after 48 hours of incubation. This stimulation is likely due to an increase in bioavailable nutrients from a UVR-DOM interaction (Wetzel et al. 1995; Gustavson et al. 2000). It appears that previous exposure to UVR does not lead to adaptative photoprotection in bacteria. Gustavson et al. (2000) found higher sensitivity to UVB in bacterial communities that had been exposed to enhanced UVB radiation for several days compared to communities that were screened from or exposed to ambient UVB levels. Herndl et al. (1993) also showed that bacteria within and below the euphotic zone exhibited the same sensitivity to UVB. Together, these studies suggest that the interaction of UVR and bacterioplankton from different depths in the mixed layer is not important. Also, we cannot say if the stimulation in bacterial production would have continued with a longer incubation (>48h), as most long-term studies have shown inhibition of bacterial production after UVR exposure (e.g. Aas et al. 1996; Sommaruga et al. 1999).

### **Stratification history and previous exposure**

Previous UVR exposure and stratification history are important in explaining a portion of our results. We examined the stratification and UVB history (2-day average prior to its commencement) of each experiment with the UVPE values that we calculated. The lowest UVPE values are for experiments 1, 4 and 6 (Fig. 5.5). In two experiments (1 and 4), low UVPE values were observed and no algal growth was found in either near-surface or base algal samples



regardless of UVR treatment (Fig. 5.2). In experiments 1 and 4, initial photosynthetic rates were higher in surface phytoplankton suggesting that the algal population was not photoinhibited, and had increased their photosynthesis to accommodate the lower irradiance. However, this is not the case for experiment 6, which also had a low UVPE value. Another factor, such as taxonomic composition, must play an important role in determining UVR sensitivity to natural algal assemblages. Others have shown that phytoplankton exposed to UVA and UVB early in the ice-free season (May, June) are more sensitive to UVR than later (July, August) probably because UVR tolerant algal assemblages or physiological adaptation occur later in the season (Gala and Giesy 1991; Smith et al. 1998; Xenopoulos et al. 2000; Xenopoulos et al., in press). Finally, in L302S the low UVPE value from experiment 1 was associated with cooler surface air temperatures and high winds which may have favored entrainment of algae from the metalimnion into the mixed layer (Fee 1976). Metalimnetic algal blooms in L302S have been previously documented (Fee 1976) and consist mainly of chrysophytes (*Dinobryon sertularia* and *Uroglena americana*; Fee et al. 1977). These species are expected to be particularly sensitive to high light exposures (Xenopoulos et al. 2000).

The highest values of UVPE were for experiments 2 and 5. These values were associated with high UVB and stable stratification conditions. We expected that the base phytoplankton would be hypersensitive to the incubation in shallow waters and high irradiance. Indeed, we found slower growth or death in the base phytoplankton samples of experiments 2 and 5 (Fig. 5.2). However, we found no inhibition of base phytoplankton photosynthesis for experiment 2. In experiment 5, rates quickly returned to the pre-exposure values (Fig. 5.3). It is possible that base phytoplankton cells photoadapted and adjusted their photosynthetic rates to accommodate the new higher irradiances. Although the UVPE values prior to the experiment were high, it is also possible that these algae were located in the near-surface waters one or two days prior to the commencement of the experiment but were completely mixed at night by convective cooling. If so, the phytoplankton may have been acclimated to the high irradiances found in surface waters.

Variation in UV sensitivity in phytoplankton is consistent with acclimation to higher exposure (Neale et al. 1998a,b; Roos and Vincent 1998). In general, the highest sensitivity is found in assemblages that have a history of low light exposure. Similarly, transplantation studies of benthic macroalgae from base to shallow waters have shown that their vertical distribution in nature correlates well with their sensitivity to UVR (Larkum and Wood 1993; Karsten et al. 2001; Gómez et al. 1998). Vertical zonation of phytoplankton is more dynamic and can change on



shorter time scales depending on the wind speed, solar radiation and water column stability (Lewis et al. 1984a,b).

## Conclusions

The relationships between UVR and phytoplankton from different depths of the mixed layer are more complex than originally envisioned. Nevertheless, the frequent and persistent formation of daytime near-surface thermoclines (Xenopoulos and Schindler, in press, chapter 3) can have some negative effects on plankton communities. However, *UVR effects do not appear to be ubiquitous* and it is clear that caution is warranted when drawing conclusions from UVR studies that only include a single experiment or measurement in time.





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## 6. REGULATION OF BOREAL LAKE PHYTOPLANKTON BY UV RADIATION: EVIDENCE FROM SEASONAL PATTERNS IN ALGAL PIGMENTS.

### INTRODUCTION

At an ecosystem level, it is important to know the relative susceptibility of planktonic organisms to ultraviolet radiation (UVR) because it could drive changes in taxonomic composition and important ecological processes. Most of the reported UVR effects on plankton are for single-species cultures under laboratory conditions or constrained multiple-species systems in mesocosms. The relevance of UVR effects observed at small spatial and time scales to whole ecosystems remains a matter of speculation (Mostajir et al. 2000). This is especially so when one considers the high likelihood of strong interactions between UVR and other environmental factors that are poorly captured in laboratory and mesocosm studies. For example, UVR interacts with mixing (Neale et al. 1998; Xenopoulos et al. 2000), temperature (Lesser 1996; Rae and Vincent 1998; Roos and Vincent 1998; Xenopoulos et al. 2000; Kelly 2001), nutrients (Behrenfeld et al. 1994; Bergeron and Vincent 1997; Hessen and Alstad Rukke 2000; Xenopoulos et al. in press) and anthropogenic stressors (Schindler et al. 1996; Yan et al. 1996), which all vary at different temporal and spatial scales within lake pelagic zones. Given the number and complexity of potential interactions, single-factored UVR studies are grossly inadequate for understanding UVR effects on ecosystem-level processes (Schindler 1998).

*Ecosystem-level UVR studies for plankton* are few in number (Vernet 2000) but have generally found an important role of UVR in lakes. At long time scales, UVR can exert a strong control over whole lake ecosystems as shown by paleolimnological evidence (Leavitt et al. 1997). This long-term control appears connected to fluctuating levels of dissolved organic carbon (DOC; Schindler et al. 1996; Pienitz and Vincent 2000; Williamson et al. 2001), a strong attenuator of UVR (Scully and Lean 1994; Morris et al. 1995; Schindler et al. 1996). At a shorter time scale (one growing season), Xenopoulos et al. (2000) showed that UVR can control algal community composition, particularly during times of weak mixing. Beyond this, however, studies of lake plankton of different susceptibility to UVR effects have yet to be completed for lakes varying in important physical and chemical factors. There are also no studies on UVR effects on species composition under natural conditions.





In this study, we used phytoplankton pigments as indicators of algal biomass, taxonomic composition, and physiological condition to examine how ambient UVR influences algal community composition under natural conditions during the growing season. Plankton placed inside 'bags' are generally inhibited by UVR (UVA more than UVB), particularly when restrained to shallow depths (e.g. Milot-Roy and Vincent 1994). It is not clear whether or not UVR effects occur in whole lakes where circulation is less restrained and changes in pigments or algal species could dampen UVR effects.

Several types of chlorophylls and carotenoids are generally found in phytoplankton, depending on the taxonomic composition of the community (see Table 6.1). Chlorophylls, which are used for photosynthesis, can be bleached under high UVR (Smith et al. 1980). In contrast, carotenoids, which are accessory to photosynthesis, provide strong photoprotection of algae (Roy 2000). They act as antioxidants by removing free-radicals formed by high irradiance and by dissipating excess light energy (e.g. Schubert et al. 1994; Vincent and Roy 1993). It is thus expected that carotenoid:chl ratios will increase under high irradiance as algae shift from photosynthesis to photoprotection (Paerl et al. 1983; Anning et al. 2000; see review by Vernet 2000). Some algae also produce pigments that are efficient UVR screens and indicate UV exposure (for example: scytonemin and mycosporine-like amino acids; Garcia-Pichel and Castenholz 1991; Sommaruga and Garcia-Pichel 1999; Whitehead and Vernet 2000).

Little is known about how UVR influences the taxonomic composition of phytoplankton communities in lakes. Diatoms and chrysophytes appear to be the most sensitive of phytoplankton to UVR-exposure (Ekelund 1994; Davidson et al. 1996; Leavitt et al. 1999; Vinebrooke and Leavitt 1999; Xenopoulos et al. 2000), while Cyanobacteria and chlorophytes appear to be more resilient (Vinebrooke and Leavitt 1999; Xenopoulos et al. 2000). However, this may be an oversimplification, because sensitivities within a taxon are highly variable in space and time (Calkins and Thordardottir 1980; Xiong et al. 1997). Here, we examine whether seasonal changes in phytoplankton taxonomic composition, inferred from pigment tracers, relate to daily UV flux.

The nutritional status of phytoplankton can alter their tolerance to UVR and their capacity for recovering from UVR damage (see review by Vernet 2000). Higher temperature can also increase metabolic rates and improve UVR repair mechanisms (Roos and Vincent 1998). Through the growing season in boreal lakes, water temperature increases at the same time as UVR flux, while





nutrients decrease in concentration. All these concurrent changes will likely be important in explaining UVR effects on the phytoplankton.

Finally, DOC mediates UVR exposure of plankton communities (Schindler et al. 1996). It is generally assumed that organisms found in high DOC lakes will be less sensitive to UVR fluctuations than those found in more transparent lakes (e.g. West et al. 1999). However, others have shown that populations from highly exposed habitats (shallow, transparent waters, high elevation lakes, tropical lakes) *can be more tolerant to UVR* than populations from better-protected environments (Helbling et al. 1992; Moeller 1994) because they are acclimated to higher irradiances. Negative effects of UVR have been observed in brown, humic ( $\text{DOC} > 5 \text{ mg L}^{-1}$ ) lakes (Xenopoulos et al. 2000; Kaczmarska et al. 2000). Although humic lakes have less UVR penetration, they also exhibit shallower mixing depths (Mazumder et al. 1990, Perez-Fuentetaja et al. 1999; Snucins and Gunn 2000) and higher frequency of near-surface thermoclines (Xenopoulos and Schindler in press), both factors that contribute to higher UVR exposure.

We conducted a survey of phytoplankton pigments over two summers in lakes differing in transparency and nutrient content. We then related day-to-day fluctuations in UVB (in this study correlated with UVA and PAR), temperature and mixing depth with daily fluctuations in phytoplankton. We incorporated both a mixing parameter and high irradiances. We also examined changes in photoprotective pigments. We show that mesohumic lakes are the most sensitive lakes to UVR exposure, while oligotrophic, transparent lakes exhibit few negative UVR effects.

## METHODS

### Study Site

This study was completed in the boreal forest of northwestern Ontario at the Experimental Lakes Area (ELA; 49°40'N, 93°44'W). We monitored five lakes, L224, L225, L227, L302S and L305 (Table 6.2), over the course of two summers, 1998 and 1999. These lakes were chosen for differences in lake size, water clarity and physico-chemical properties. Some physico-chemical parameters are presented in Table 6.2.



L224 is a clear, oligotrophic lake. The primary algal taxonomic groups in this lake are chrysophytes (*Chrysochromulina*, *Dinobryon*) and diatoms (*Tabellaria*, *Cyclotella*). L224 has been a reference lake for 30 years, with only some radioisotopic tracer studies done in 1976 (Hesslein et al. 1980). L305 is also a clear, oligotrophic lake but larger in size than L224. The lake has a deep euphotic and mixed zone. The water column has persistently low nutrients in the surface and a deep hypolimnetic chlorophyll maximum develops (*Uroglena*).

L225 is a highly humic and shallow lake. Experimental manipulations of this lake include pulse acidification with HCl in the 1980s and 1990s. Macrophytes (*Nuphar*) are important. Archived taxonomic data from L225 show that it has a high biomass of *Gymnodinium* (Peridinae). L227 has been artificially enriched with phosphorus since 1969. Nitrogen was also added from 1969 to 1989 (Schindler et al. 1987; Findlay et al. 1994). The cryptophytes and chrysophytes present naturally in this lake have been replaced by chlorophytes and Cyanobacteria. This lake also has diurnal variations in dissolved inorganic carbon concentrations resulting from high phytoplankton production (Schindler and Fee 1973). The phytoplankton is typically carbon-limited by mid-morning. The lake becomes anoxic below 4 m by mid-summer (Schindler 1971; ELA unpublished records). L225 and L227 are small lakes that are isolated from direct wind-induced turbulence.

L302 was part of a eutrophication study in the 1970s (Schindler et al. 1978). The south basin of L302 (L302S) has been artificially acidified since 1982. The pH was reduced from 6.7 (1982) to 4.5 (1989-1991). The lake is recovering since 1992 and the pH has been held at 6.0 since 1996 (Findlay et al. 1999). Many chemical and biological changes followed lake acidification (Schindler et al. 1991), some of which are UVR-related (Schindler et al. 1996; Donahue et al. 1998; Leavitt et al. 1999). During acidification, DOC concentration was reduced to  $< 1 \text{ mg L}^{-1}$  (Schindler et al. 1996) and DOC quality altered, increasing UV penetration by 800% (Donahue et al. 1998). In response, the concentration of UV-protective pigments increased (Leavitt et al. 1999). Chrysophytes and diatoms, naturally present in the lake before acidification, were replaced with filamentous greens and dinoflagellates (Findlay et al. 1999, Leavitt et al. 1999).

## Lake sampling

Lakes 224, 225, 227 and 305 were sampled in 1998. In 1999, Lakes 224 and 302S were sampled. Sampling started in June and continued until the end of July in 1998. In 1999, sampling started in



mid-May and ended in early August. Lakes were usually sampled every day to every 5 days. Sampling occurred between 900 and 1100 each morning over the deepest point of the lake. Water from near the surface of the lake (~20 cm) was collected using a Van Dorn sampling bottle (1998) or a peristaltic pump (1999) and placed into dark polycarbonate bottles until further processed (within 2-hours).

### **Temperature, PAR and Ultraviolet Radiation measurements**

Hobo-Temp temperature data loggers were installed *in situ*, at every half meter, to monitor temperature changes in the lakes. Photosynthetically active radiation (PAR) was determined daily with a Li-Cor quantum sensor and incident UV radiation by means of UVA and UVB sensors as described in Xenopoulos et al. (in press, see chapter 4) at the met site. Stratospheric ozone concentration above ELA was taken from the NASA website (<http://jwocky.gsfc.nasa.gov/TOMSMmain.html>).

### **Pigment determination**

Lake water aliquots for pigment analysis were filtered onto GF/F filters and kept in the dark at -20°C until further analysis. Carotenoids and chlorophylls were extracted (24h, 10°C, in the dark) using a standard mixture of acetone, methanol, and water (80:15:5). Extracts were filtered (0.22µm Acropore Nylon membrane) and dried in the dark using N<sub>2</sub> gas. Dried extracts were stored at -20°C under N<sub>2</sub> in the dark until pigment analysis. Pigment concentrations in the water column were determined using HPLC equipped with a Rainin C-18 column (10 cm, 5 µm particles) following the reversed-phase liquid chromatography procedure of Mantoura and Llewelyn (1983) as modified by Leavitt et al. (1989). Briefly, analytical separation was achieved by isocratic delivery of a mobile phase A for 1.5 min, a linear succession to 100% solution B (27% acetone in methanol) over 7 min, and isocratic hold for 12.5 min. Analysis of pigments (see Table 6.1) was restricted to carotenoids characteristic of cryptophytes (alloxanthin), dinoflagellates (peridinin) mainly diatoms (diatoxanthin and diadinoxanthin), diatoms with chrysophytes and some dinoflagellates (fucoxanthin), chlorophytes and Cyanobacteria (lutein, zeaxanthin), cyanobacteria (echinenone, canthaxanthin), filamentous or colonial Cyanobacteria (myxoxanthophyll) and N<sub>2</sub>-fixing Cyanobacteria (aphanizophyll). Chlorophyll *a* (all algae), *b* (chlorophytes), *c* (chromophytes) and pheophytins *a* and *b* were also quantified. The grazer pigment pheophorbide *a* (chlorophyll *a* degraded by grazers) was also quantified. An unknown





compound (or compounds) was labeled as characteristic of high UV environments (labeled “S”) because of its absorbance characteristics and similarities with scytonemin. This compound runs immediately after the initial injection peak at ~2 minutes and before the chlorophyll *c* peak and has absorbance maximum near 400 nm. This pigment was found in significant concentrations only in L227. Pigments were quantified using authentic standards, obtained from the US-EPA. Unfortunately the method used here did not allow us to measured mycosporine-like amino acids (MAAs).

**Table 6.1.** Chlorophylls and carotenoids measured in this study and the specific taxa they are found to associate with.

Pigment	Taxa
<u>Chlorophylls</u>	
Chlorophyll <i>a</i>	All algae
Chlorophyll <i>b</i>	chlorophytes
Chlorophyll <i>c1</i> and <i>c2</i>	chromophytes
Pheophytin <i>a, b</i>	Degradation product
<u>Carotenoids</u>	
Alloxanthin	cryptophytes
Aphanizophyll	N <sub>2</sub> -fixing Cyanobacteria
Canthaxanthin	Cyanobacteria
Diatoxanthin/ Diadinoxanthin	diatoms
Fucoxanthin	chromophytes
Lutein-Zeaxanthin	chlorophytes-Cyanobacteria
Myxoxanthophyll	Filamentous or colonial Cyanobacteria
Peridinin	dinoflagellates
Violaxanthin	chromophytes
β-carotene	All algae

**Data analysis**

Stratification and UVR exposure intensity index.

We defined an index of previous UVR exposure (UVPE) that takes into account the UVA and UVB at the surface of the lake ( $J\ m^{-2}$ ) and a stratification parameter PE ( $J\ m^{-2}$ ) as:

$$UVPE = UVR * PE, \tag{1}$$

where UVR is the sum of UVB and UVA ( $J\ m^{-2}$ ), and PE ( $J\ m^{-2}$ ) is equivalent to the amount of energy required to vertically homogenize the water layer (Nelson et al., 1989). PE is defined by:





$$PE = (1/12) \Delta\rho g z^2, \quad (2)$$

where  $g$  ( $\text{m s}^{-2}$ ) is the acceleration due to gravity,  $\Delta\rho$  ( $\text{kg m}^{-3}$ ) is the density gradient between the surface and bottom of the mixed layer ( $\rho_{\text{bottom}} - \rho_{\text{surface}}$ ) and  $z$  (m) is the depth of the mixed layer. A high PE number would indicate very stable stratification and the presence of near-surface thermoclines (low mixing).

We found the product (as opposed to the sum) of PE and UVR to give a more accurate description of the light/stratification history because of the importance of intermediate UVR and PE values. Hence, two values of opposite extremes (i.e. high PE but low UVR) are weighted less than two intermediate values (intermediate UVR and PE). Two high values (high UVR and low mixing conditions or high PE) yield the maximum number. Data for the index were collected for the two days prior to the commencement of the experiment.

#### Relationships between phytoplankton pigment concentrations and environmental factors.

Pigment concentrations were log transformed prior to statistical analysis to stabilize the variance and normalize their distribution. Correlation and regression analysis were performed using JMP (SAS Institute 1996).

Pearson-product moment correlation coefficients with Bonferroni-adjusted probabilities were used to detect significant environmental covariables. Simple linear regression analyses were performed to detect significant relationships between pigment concentrations and the following environmental variables: UVB, UVPE, temperature and mixing depth. Because sampling occurred in the morning (900 and 1100) and UVB damage is a result of the cell's light history, 3-day running averages of UVB and UVPE were used (the sampling day and the two days before; Xenopoulos et al. 2000). UVPE was also log-transformed to normalize its distribution. Autocorrelations among our environmental variables negated the use of multiple regressions in this study.



**Table 6.2.** Physico-chemical characteristics of lakes in this study.

	224	225	227	302S	305
$Z_{\max}$ (m)	27.4	4.0	10.0	10.6	32.7
$A_0$ (ha)	25.5	2.0	5.0	10.9	52.0
Thermocline (m)	6.0	1.5	3.0	5.0	7.0
$K_{dPAR}$ ( $m^{-1}$ )	0.24	1.63	1.50	0.60	0.34
DOC ( $mg\ L^{-1}$ )	3.2	9.6	11.4	4.2	3.8
1% UVB penetration (m)	1.5	0.17	0.12	0.75	1.0
Chlorophyll <i>a</i> ( $\mu g\ L^{-1}$ )	0.5-1.5	5.9-11	50-200	0.8-2.0	1.0-2.0
TP ( $\mu g\ L^{-1}$ )	4	12	20-400	8	3

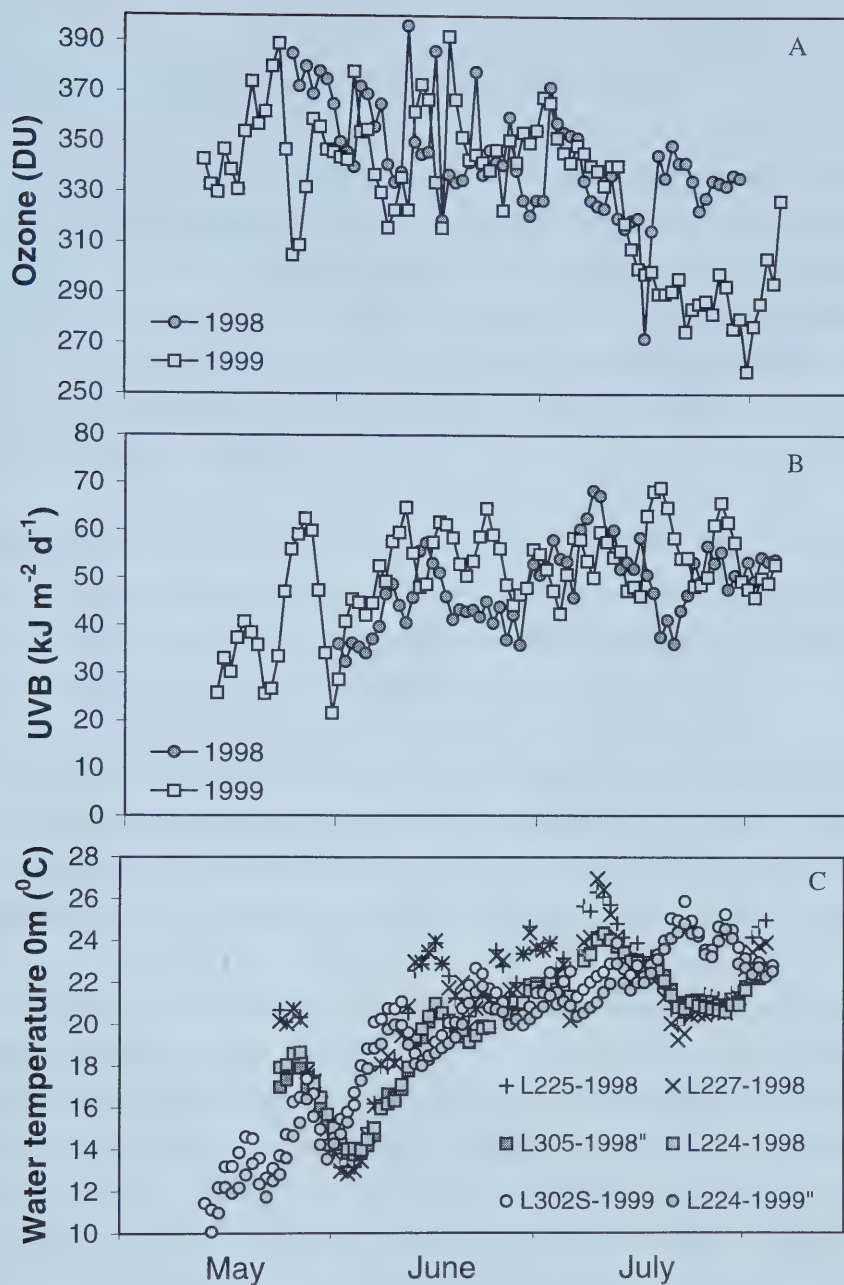
## RESULTS

### Stratospheric Ozone, UVB and Temperature.

Stratospheric ozone concentration decreased from spring until summer both in 1998 and 1999 (Fig. 6.1a). In particular in 1999, there was a significant drop in ozone concentration later in the summer from 330 DU to ~270 DU (Fig. 6.1a). Ozone concentration was not related to any of the pigments in this lake and is not further discussed.

Incident UVB varied from day to day but generally increased from spring until late summer (Fig. 6.1b). UVB reaching the surface was generally higher in 1999 than in 1998. This is likely the result of unusually high rainfall in 1998, which was one of the wettest summers on record at the ELA (Beaty, K., Freshwater Institute, unpublished data). UVA showed a seasonal increase similar to UVB (not shown). UVA and UVB were highly correlated both in 1998 and 1999 ( $r = 0.98$ ,  $P < 0.0001$  in 1998;  $r = 0.95$ ,  $P < 0.0001$  in 1999). Surface PAR was also highly correlated with UVB ( $r = 0.90$ ,  $P < 0.0001$  in 1998;  $r = 0.84$ ,  $P < 0.0001$  in 1999). Stratospheric ozone concentration was correlated with UVB but the variance explained was low ( $r = -0.26$ ,  $P = 0.0412$  in 1998;  $r = -0.30$ ,  $P = 0.0164$ ). Lake surface temperatures increased from spring until summer (Fig. 6.1c). Lakes with high DOC (L225 and L227) exhibited greater fluctuations in their surface temperature than clearer lakes (Fig. 6.1c). UVB was correlated with the lake temperature at the surface ( $r = 0.36, 0.37, 0.42, 0.44$ ,  $P < 0.01$  for L305, L224, L227 and L225 in 1998 respectively;  $r = 0.42$ ,  $P < 0.0001$  for both L302S and L224 in 1999).





**Figure 6.1.** a) Stratospheric ozone concentration over ELA in 1998 and 1999 b) UVB measured at the surface in 1998 and 1999 throughout the study period. c) Water temperature measured at the surface of the lakes in 1998 and 1999.



### Phytoplankton community structure in the different lakes.

In 1998, L305 and L224 had similar phytoplankton community structures. Both contained relatively high concentrations of pigments characteristic of diatoms and chrysophytes throughout the summer (Fig. 6.2a). In L224, fucoxanthin (diatoms and chrysophytes) was high early in the summer and decreased at the expense of the pigments lutein-zeaxanthin (chlorophytes and Cyanobacteria). Fucoxanthin was the most abundant carotenoid but generally co-varied with other carotenoids and chlorophylls characteristic of chromophytic algae (e.g. chl *c*, diatoxanthin and violaxanthin, not shown).

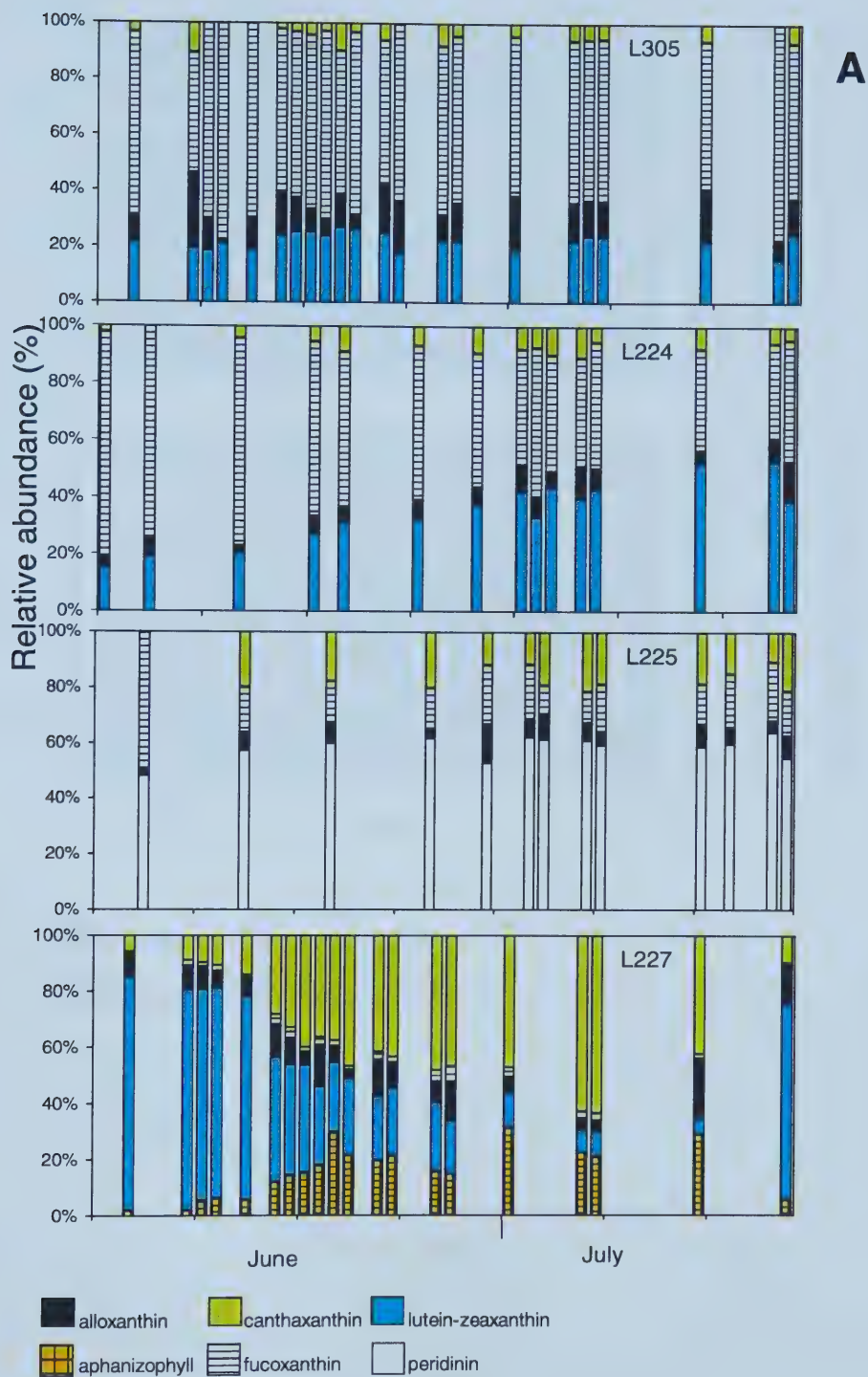
L225 was mainly dominated by dinoflagellates as indicated from high concentrations of the carotenoid, peridinin, throughout the summer. High concentrations of chlorophyll *c* were also found in L225. Cyanobacteria, chlorophytes and chromophytes also contributed to phytoplankton biomass but less so than the dinoflagellates (Fig. 6.2a).

L227's pigment composition changed from a dominance of chlorophytes and Cyanobacteria (lutein-zeaxanthin) in early summer to that of almost only Cyanobacteria (canthaxanthin), filamentous Cyanobacteria (myxoxanthophyll, not shown) and N<sub>2</sub>-fixing Cyanobacteria (aphanizophyll). Very few cryptophytes and chromophytes were present in L227 (Fig. 6.2a).

In 1999, high concentrations of fucoxanthin suggest that diatoms and chrysophytes were the primary classes of phytoplankton in L302S and L224. In L224, the community structure changed from domination by diatoms and chrysophytes in early summer to green algae, Cyanobacteria and some chromophytes, as was observed in 1998 (Fig. 6.2b). L302S's phytoplankton community always consisted mainly of chromophytes and dinoflagellates throughout the summer, although chlorophytes (lutein-zeaxanthin) increased in concentration slightly (Fig. 6.2b).







**Figure 6.2.** Relative abundance of the major pigments measured in the study lakes in a) 1998 and b) 1999.



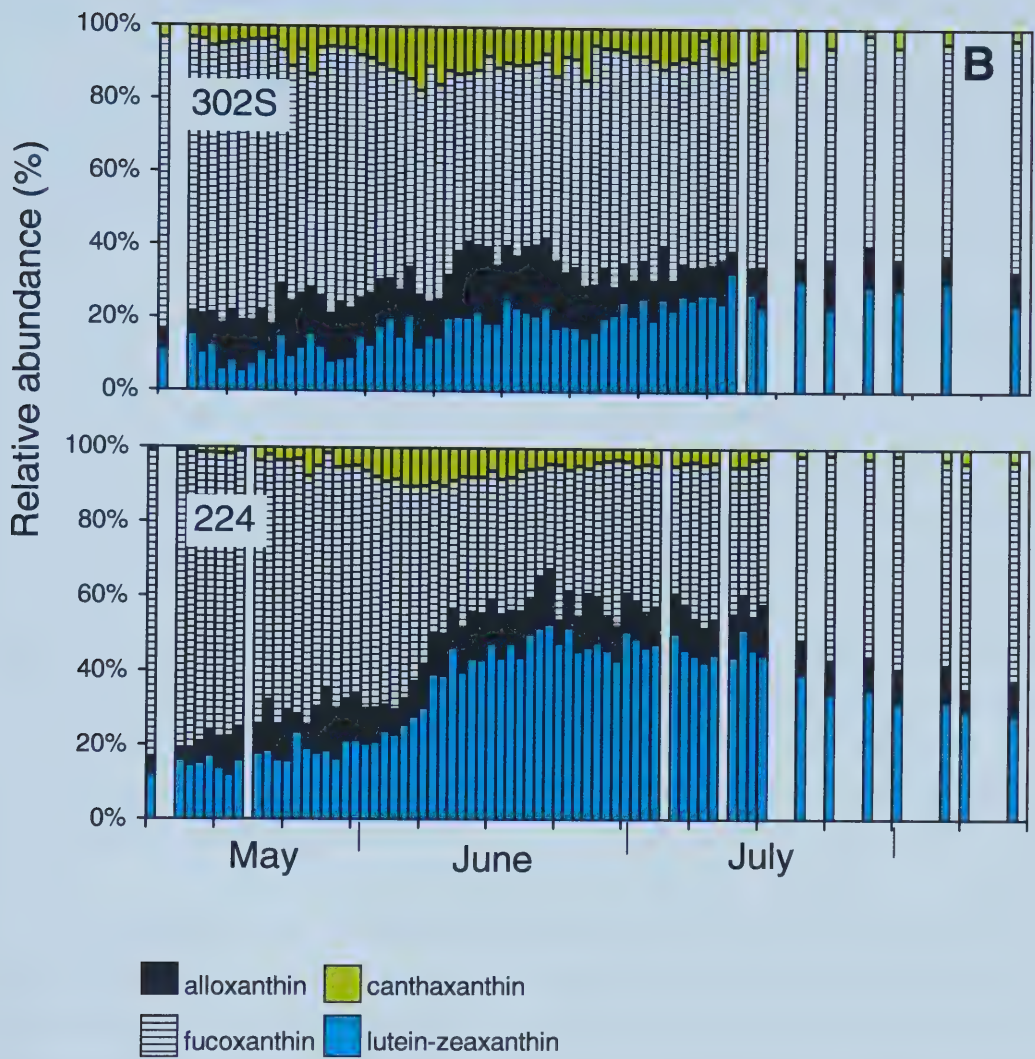


Figure 6.2b) continued



## Phytoplankton pigment concentrations and their relationships with environmental factors.

In both years, pigment concentrations was related to UVB (excluding ratios and the grazer pigment pheophorbide) in 30 of 89 statistical tests (Tables 6.3-6.8). UVPE was related to pigment concentrations in 38 of 89 statistical tests (Tables 6.3-6.8). Temperature was related to pigment concentrations in 47 cases and mixing depth in 22 of 89 cases (Tables 6.3-6.8).

The most common pigments (chlorophylls, fucoxanthin, canthaxanthin, lutein-zeaxanthin and alloxanthin) from the different lakes varied in their responses to UVB, UVB and mixing (UVPE), temperature and mixing depth. Statistical tests of all pigments are shown in Tables 6.3 to 6.8. Five pigments were selected to illustrate the nature of the relationships between pigment concentrations and the four environmental variables (Fig. 6.3 and 6.4). Below is a summary of some relationships.

Phytoplankton from L224 and L305, two of the clearest lakes at ELA, had few relationships with our environmental variables (Tables 6.3 and 6.4). For L305, only one phytoplankton pigment (chl *c1*) showed a significant relationship with UVB, one (pheophytin *a*) with UVPE and one (pheophytin *a*) with temperature. No significant relationships between mixing depth and pigment concentrations were found (Table 6.3).

In L224 in 1998, fucoxanthin (chromophytes) and chl *b* (chlorophytes) were negatively related with UVB (Table 6.4). No other significant relationships with UVB were found. Cryptophytes (alloxanthin) and filamentous Cyanobacteria (myxoxanthophyll) increased in concentration with increasing UVPE (Table 6.4). Carotenoids found in diatoms (fucoxanthin and violaxanthin) were negatively related to temperature while chlorophytes and Cyanobacteria (lutein, zeaxanthin and canthaxanthin) were positively related to temperature (Table 6.4). No significant relationships were found between mixing depth and pigment concentration in L224 in 1998 (Table 6.4).

In L225, pigments characteristic of dinoflagellates (peridinin, chl *c*), Cyanobacteria (canthaxanthin), chlorophytes (chl *b*) and cryptophytes (alloxanthin) increased in concentration with increasing UVPE and/or UVB (Table 6.5). No negative relationships between pigments and UVB or UVPE were found. Pigments characteristic of diatoms and chrysophytes were not affected by UVB and UVPE (Table 6.5). Most pigments measured in L225 were positively related to temperature (Table 6.5). Dinoflagellates (peridinin, chl *c*), chlorophytes (lutein-





zeaxanthin, chl *b*) and Cyanobacteria (myxoxanthophyll, canthaxanthin, echinenone), increased in concentration when the mixing depth was shallower (Table 6.5).

A pigment similar to the photoprotective scytonemin was found in moderately high concentrations in L227 (label S). Not surprisingly, the concentration of S increased with increasing irradiance, UVPE and temperature (Table 6.6). Pigments characteristic of diatoms, chrysophytes and cryptophytes were not related to UVB, UVPE and temperature (Table 6.6). In general, Cyanobacteria (canthaxanthin) increased in concentration with UVB and UVPE (Table 6.6). N<sub>2</sub>-fixing Cyanobacteria (aphanizophyll) also increased with UVB and UVPE (Table 6.6). On the other hand, filamentous Cyanobacteria (myxoxanthophyll) decreased with increasing UVB and UVPE (Table 6.6). Temperature was positively associated with all pigments found in Cyanobacteria and with chl *a* and *c* (Table 6.6). As L227's mixing depth increased, chlorophylls decreased in concentration along with pigments found in Cyanobacteria (Table 6.6).

In 1999, pigments indicating chrysophytes and diatoms (chl *c*'s, and fucoxanthin) from L224 were negatively related to UVB but the variance explained in these relationships was low (always less than 20%; Table 6.7). The concentration of carotenoids found in chlorophytes and Cyanobacteria increased with UVB but again the variance explained by these relationships was low (Table 6.7). UVPE was negatively related to chl *b*, pheophytin *a*, alloxanthin and fucoxanthin and positively with canthaxanthin (Table 6.7). Chlorophytes and Cyanobacteria were positively related to temperature while some chromophytic pigments were negatively related to temperature (Table 6.7). No significant relationships with pigments and mixing depth was found, except for  $\beta$ -carotene that increased in concentration as the mixing depth decreased (Table 6.7).

In L302S, chlorophytes (lutein-zeaxanthin and chl *b*) and Cyanobacteria (canthaxanthin) were not significantly related to UVB (Table 6.8). All other pigments were negatively related to UVB (Table 6.8). UVPE was also negatively correlated with most pigments but the variance explained by UVPE was lower than that explained by UVB alone (Table 6.8). Temperature was negatively correlated with most pigments in L302S. Relationships between pigment concentrations and mixing depth in L302S, where found, only explained a small percentage of the variability (Table 6.8).





## Grazing

The grazing pigment pheophorbide *a* was found at lower concentrations at high UVB and high UVPE in L305 and L224 (Tables 6.3, 6.4 and 6.7). No significant relationships with the grazer pigment were found in L225 and L302S (Table 6.5 and 6.8). Pheophorbide was not measured in L227.

## Phytoplankton pigment ratios and totals

Only the most common carotenoids (fucoxanthin and lutein-zeaxanthin) were chosen for ratio relationships. In L305, the ratios between chl *a* and fucoxanthin, lutein-zeaxanthin and total carotenoids decreased as the mixing depth increased (Table 6.3) indicating that the carotenoids increased their concentration while chl *a* decreased under shallow mixing conditions. No other significant relationships were found. In L224 (1998), total carotenoids increased in concentration with increasing UVPE (Table 6.4) and temperature positively affected the ratios of chl *a*:fucoxanthin but negatively affected chl *a*:lutein-zeaxanthin (Table 6.4). No significant ratio changes were found in L225 with UVB, UVPE or mixing depth (Table 6.5). However total carotenoids and total chlorophylls increased with increasing temperature (Table 6.5). The ratios between chl *a* and fucoxanthin, lutein-zeaxanthin and total carotenoids increased with increasing UVB, UVPE and temperature in L227 (Table 6.6).

In 1999, total chlorophylls were negatively related to UVB, UVPE and temperature in L224 (Table 6.7). The ratios of chl *a* to lutein-zeaxanthin and total carotenoids decreased with increasing UVB in L224 and L302S (Tables 6.7 and 6.8). In L302S, total carotenoids decreased with increasing UVB and UVPE but increased with temperature and mixing depth (Table 6.8).



**Table 6.3.** Summary of relationships between pigment concentrations and surface UVB, UVPE, temperature at the surface and mixing depth for L305. Simple linear regression analysis was performed using  $\log_{10}$ -transformed pigment and UVPE data. NS indicates a relationship that was found to be non significant. Where relationships were significant ( $P < 0.05$ ),  $r^2$ ,  $P$  value, and in parenthesis the direction of the relationship (+ = positive and – = negative) are shown.

Pigment	UVB ( $\text{kJ m}^{-2} \text{d}^{-1}$ )	Log UVPE ( $\text{J m}^{-2} \text{s}^{-1}$ )	Temp. 0m ( $^{\circ}\text{C}$ )	Mixing Depth (m)
<b><u>Chlorophylls</u></b>				
Chl <i>a</i>	NS	NS	NS	NS
Chl <i>b</i>	NS	NS	NS	NS
Chl <i>c1</i>	(–)	NS	NS	NS
$r^2$	0.23			
$P$	0.0238			
Chl <i>c2</i>	NS	NS	NS	NS
Pheophytin <i>a</i>	NS	(–)	(–)	NS
$r^2$		0.29	0.22	
$P$		0.0084	0.0293	
<b><u>Carotenoids</u></b>				
Alloxanthin	NS	NS	NS	NS
Canthaxanthin	NS	NS	NS	NS
Diatoxanthin	NS	NS	NS	NS
Fucoxanthin	NS	NS	NS	NS
Lutein-Zeaxanthin	NS	NS	NS	NS
Myxoxanthophyll	NS	NS	NS	NS
Violaxanthin	NS	NS	NS	NS
$\beta$ -carotene	NS	NS	NS	NS
<b><u>Grazer pigment</u></b>				
Pheophorbide	(–)	(–)	(–)	NS
$r^2$	0.23	0.29	0.18	
$P$	0.0226	0.0104	0.0488	
<b><u>Ratios and totals</u></b>				
Chl <i>a</i> :fucoxanthin	NS	NS	NS	(–)
$r^2$				0.18
$P$				0.0418
Chl <i>a</i> :lutein-zeaxanthin	NS	NS	NS	(–)
$r^2$				0.25
$P$				0.0177
Tot. carotenoid	NS	NS	NS	NS
Chl <i>a</i> : tot. carotenoid	NS	NS	NS	(–)
$r^2$				0.30
$P$				0.0089
Tot. chlorophylls	NS	NS	NS	NS



**Table 6.4.** Summary of relationships between pigment concentrations and surface UVB, UVPE, temperature at the surface and mixing depth for L224 in 1998. Simple linear regression analysis was performed using  $\log_{10}$ -transformed pigment and UVPE data. NS indicates a relationship that was found to be non significant. Where relationships were significant ( $P < 0.05$ ),  $r^2$ ,  $P$  value, and in parenthesis the direction of the relationship (+ = positive and - = negative) are shown.

Pigment	UVB ( $\text{kJ m}^{-2} \text{d}^{-1}$ )	UVPE ( $\text{J m}^{-2}$ ) <sup>2</sup>	Temp 0m ( $^{\circ}\text{C}$ )	Mixing Depth (m)
<b><u>Chlorophylls</u></b>				
Chl <i>a</i>	NS	NS	NS	NS
Chl <i>b</i>	(-)	NS	NS	NS
$r^2$	0.54			
$P$	0.0028			
Chl <i>c1</i>	NS	NS	NS	NS
Chl <i>c2</i>	NS	NS	NS	NS
Pheophytin <i>a</i>	NS	NS	NS	NS
<b><u>Carotenoids</u></b>				
Alloxanthin	NS	(+)	NS	NS
$r^2$		0.37		
$P$		0.0264		
Canthaxanthin	NS	NS	(+)	(-)
$r^2$			0.52	0.31
$P$			0.0023	0.0320
Diatoxanthin	NS	NS	(-)	NS
$r^2$			0.51	
$P$			0.0027	
Echinenone	NS	NS	NS	NS
Fucoxanthin	(-)	NS	(-)	NS
$r^2$	0.33		0.68	
$P$	0.0317		0.0002	
Lutein-Zeaxanthin	NS	NS	(+)	NS
$r^2$			0.54	
$P$			0.0018	
Myxoxanthophyll	NS	(+)	NS	NS
$r^2$		0.42		
$P$		0.0163		
Violaxanthin	NS	NS	NS	NS
$r^2$				
$P$				
$\beta$ -carotene	NS	NS	NS	NS
<b><u>Grazing pigment</u></b>				
Pheophorbide	(-)	NS	NS	NS
$r^2$	0.49			
$P$	0.0050			
<b><u>Ratios and totals</u></b>				
Chl <i>a</i> :fucox	NS	NS	(+)	NS
$r^2$			0.43	
$P$			0.0083	
Chl <i>a</i> :lutein-zeaxanthin	NS	NS	(-)	NS
$r^2$			0.37	
$P$			0.0162	
Total carotenoids	NS	(+)	NS	NS
$r^2$		0.39		
$P$		0.0223		
Chl <i>a</i> : tot. carot.	NS	NS	NS	NS
Total chlorophylls	NS	NS	NS	NS



**Table 6.5.** Summary of relationships between pigment concentrations and UVB, UVPE, temperature at the surface and mixing depth for L225 in 1998. Simple linear regression analysis was performed using  $\log_{10}$ -transformed pigment and UVPE data. NS indicates a relationship that was found to be non significant. Where relationships were significant ( $P < 0.05$ ),  $r^2$ ,  $P$  value, and in parenthesis the direction of the relationship (+ = positive and - = negative) are shown.

Pigment	UVB ( $\text{kJ m}^{-2} \text{d}^{-1}$ )	Log UVPE ( $\text{J m}^{-2}$ )	Temp. 0m ( $^{\circ}\text{C}$ )	Mixing depth (m)
<b><u>Chlorophylls</u></b>				
Chl <i>a</i>	NS	NS	NS	NS
Chl <i>b</i>	(+)	(+)	(+)	(-)
$r^2$	0.36	0.37	0.52	0.42
$P$	0.0315	0.0285	0.0057	0.0160
Chl <i>c1</i>	NS	NS	(+)	NS
$r^2$			0.66	
$P$			0.0007	
Chl <i>c2</i>	NS	(+)	(+)	(-)
$r^2$		0.29	0.81	0.29
$P$		0.0453	<0.0001	0.05
Pheophytin <i>a</i>	NS	NS	NS	NS
<b><u>Carotenoids</u></b>				
Alloxanthin	NS	(+)	(+)	(-)
$r^2$		0.48	0.79	0.40
$P$		0.0090	<0.0001	0.0210
Aphanizophyll	NS	NS	NS	NS
Canthaxanthin	(+)	(+)	(+)	(-)
$r^2$	0.38	0.47	0.76	0.66
$P$	0.0281	0.01	0.0001	0.0007
Diatoxanthin	NS	NS	(+)	NS
$r^2$			0.31	
$P$			0.0463	
Echinenone	(+)	(+)	(+)	(-)
$r^2$	0.31	0.35	0.56	0.42
$P$	0.05	0.0345	0.0031	0.0160
Fucoxanthin	NS	NS	(+)	NS
$r^2$			0.57	
$P$			0.0028	
Lutein-Zeaxanthin	NS	(+)	(+)	NS
$r^2$		0.33	0.63	
$P$		0.0406	0.0012	
Myxoxanthophyll	NS	NS	(+)	NS
$r^2$			0.40	
$P$			0.0213	
Peridinin	(+)	(+)	(+)	(-)
$r^2$	0.27	0.29	0.81	0.29
$P$	0.0496	0.0353	<0.0001	0.0472
Violaxanthin	NS	NS	NS	NS
$\beta$ -carotene	NS	NS	(+)	NS
$r^2$			0.46	
$P$			0.0104	
<b><u>Grazer pigments</u></b>				
Pheophorbide	NS	NS	NS	NS





Table 6.5. continued.

<u>Ratios and totals</u>				
Chl <i>a</i> :fucoxanthin	NS	NS	NS	NS
Chl <i>a</i> : lutein-zeaxanthin	NS	NS	NS	NS
Chl <i>a</i> : peridinin	NS	NS	NS	NS
Total carotenoids	NS	NS	(+)	NS
$r^2$			0.61	
$P$			0.0015	
Chl <i>a</i> : tot. carot	NS	NS	NS	NS
Total chlorophylls	NS	NS	(+)	
$r^2$			0.54	
$P$			0.0040	



**Table 6.6.** Summary of relationships between pigment concentrations and UVB, UVPE, temperature at the surface and mixing depth for L227 in 1998. Simple linear regression analysis was performed using  $\log_{10}$ -transformed pigment and UVPE data. NS indicates a relationship that was found to be non significant. Where relationships were significant ( $P < 0.05$ ),  $r^2$ ,  $P$  value, and in parenthesis the direction of the relationship (+ = positive and - = negative) are shown.

Pigment	UVB ( $\text{kJ m}^{-2} \text{d}^{-1}$ )	Log UVPE ( $\text{J m}^{-2}$ ) <sup>2</sup>	Temp. 0m ( $^{\circ}\text{C}$ )	Mixing depth (m)
<b><u>Chlorophylls</u></b>				
Chl <i>a</i>	(+)	(+)	(+)	(-)
$r^2$	0.23	0.72	0.57	0.46
$P$	0.0310	<0.0001	0.0001	0.0011
Chl <i>b</i>	NS	(+)	NS	(-)
$r^2$		0.37		0.63
$P$		0.0044		<0.0001
Chl <i>c1</i>	NS	(+)	(+)	(-)
$r^2$		0.35	0.30	0.49
$P$		0.0058	0.0127	0.0006
Chl <i>c2</i>	NS	NS	NS	NS
Pheophytin <i>a</i>	NS	NS	NS	NS
Pheophytin <i>b</i>	NS	NS	NS	NS
<b><u>Carotenoids</u></b>				
Alloxanthin	NS	NS	NS	NS
Aphanizophyll	(+)	(+)	(+)	(-)
$r^2$	0.23	0.70	0.63	0.59
$P$	0.0335	<0.0001	<0.0001	<0.0001
Canthaxanthin	NS	(+)	(-)	(-)
$r^2$		0.62	0.54	0.66
$P$		<0.0001	0.0002	<0.0001
Diatoxanthin	(+)	(+)	(+)	NS
$r^2$	0.22	0.38	0.49	
$P$	0.0365	0.0040	0.0006	
Echinenone	NS	(+)	(+)	(-)
$r^2$		0.65	0.53	0.61
$P$		<0.0001	0.0003	<0.0001
Fucoxanthin	NS	NS	NS	NS
Lutein-zeaxanthin	(-)	(-)	(-)	NS
$r^2$	0.51	0.51	0.75	
$P$	0.0004	0.0004	<0.0001	
Myxoxanthophyll	(-)	NS	(-)	NS
$r^2$	0.23		0.24	
$P$	0.0335		0.0273	
S (Scytonemin-like)	(+)	(+)	(+)	(-)
$r^2$	0.29	0.56	0.56	0.44
$P$	0.0153	0.0001	0.0001	0.0015
Violaxanthin	NS	NS	NS	NS
$\beta$ -carotene	NS	(+)	(+)	(-)
$r^2$		0.50	0.40	0.66
$P$		0.0005	0.0028	<0.0001
<b><u>Ratios and Totals</u></b>				
Chl <i>a</i> :fucoxanthin	(+)	(+)	(+)	(-)
$r^2$	0.27	0.48	0.52	0.32
$P$	0.0181	0.0007	0.0004	0.0100
Chl <i>a</i> :lutein-zeaxanthin	(+)	(+)	(+)	NS
$r^2$	0.38	0.30	0.46	
$P$	0.0035	0.0116	0.0010	



Table 6.6. continued.

Total carotenoids	NS	(+)	(+)	(-)
$r^2$		0.30	0.25	0.27
$P$		0.0126	0.0241	0.0193
Chl $a$ : tot. carotenoids	(+)	(+)	(+)	(-)
$r^2$	0.38	0.77	0.69	0.48
$P$	0.0040	<0.0001	<0.0001	0.0007
Total chlorophylls	NS	(+)	(+)	(-)
$r^2$		0.44	0.39	0.32
$P$		0.0014	0.0034	0.0090



**Table 6.7.** Summary of relationships between pigment concentrations and UVB, UVPE, temperature at the surface and mixing depth for L224 in 1999. Simple linear regression analysis was performed using  $\log_{10}$ -transformed pigment and UVPE data. NS indicates a relationship that was found to be non significant. Where relationships were significant ( $P < 0.05$ ),  $r^2$ ,  $P$  value, and in parenthesis the direction of the relationship (+ = positive and – = negative) are shown.

Pigment	UVB ( $\text{kJ m}^{-2} \text{d}^{-1}$ )	Log UVPE ( $\text{J m}^{-2}$ ) <sup>2</sup>	Temp 0m ( $^{\circ}\text{C}$ )	Mixing depth (m)
<b><u>Chlorophylls</u></b>				
Chl <i>a</i>	NS	NS	NS	NS
Chl <i>b</i>	NS	(–)	NS	NS
$r^2$		0.10		
$P$		0.0136		
Chl <i>c1</i>	(–)	NS	(–)	NS
$r^2$	0.11		0.13	
$P$	0.0076		0.0027	
Chl <i>c2</i>	(–)	NS	(–)	NS
$r^2$	0.15		0.19	
$P$	0.0016		0.0003	
Pheophytin <i>a</i>	NS	(–)	NS	NS
$r^2$		0.15		
$P$		0.0015		
<b><u>Carotenoids</u></b>				
Alloxanthin	NS	(–)	(+)	NS
$r^2$		0.16	0.19	
$P$		0.0011	0.0002	
Canthaxanthin	(+)	(+)	(+)	NS
$r^2$	0.15	0.12	0.26	
$P$	0.0015	0.0051	<0.0001	
Diadinoxanthin	NS	NS	(–)	NS
$r^2$			0.13	
$P$			0.0031	
Diatoxanthin	NS	NS	(–)	NS
$r^2$			0.28	
$P$			<0.0001	
Fucoxanthin	(–)	(–)	NS	NS
$r^2$	0.18	0.18		
$P$	0.0005	0.0005		
Lutein-zeaxanthin	(+)	NS	(+)	NS
$r^2$	0.16		0.67	
$P$	0.0008		<0.0001	
Myxoxanthophyll	NS	NS	NS	NS
Violaxanthin	NS	NS	NS	NS
$\beta$ -carotene	NS	NS	(+)	(–)
$r^2$			0.31	0.10
$P$			<0.0001	0.0258
<b><u>Grazer pigment</u></b>				
Pheophorbide	(–)	(–)	NS	NS
$r^2$	0.20	0.33		
$P$	0.0411	0.0254		





**Table 6.7.** Continued.

<b>Ratios and totals</b>				
Chl <i>a</i> :fucoxanthin	NS	NS	(+)	NS
$r^2$			0.12	
<i>P</i>			0.0050	
Chl <i>a</i> :lutein-zeaxanthin	(−)	NS	(−)	NS
$r^2$	0.38		0.73	
<i>P</i>	<0.0001		<0.0001	
Total carotenoids	NS	NS	NS	NS
Chl <i>a</i> : tot. carotenoids	(−)	NS	(−)	NS
$r^2$	0.14		0.27	
<i>P</i>	0.0021		<0.0001	
Total chlorophylls	(−)	(−)	(−)	NS
$r^2$	0.17	0.10	0.30	
<i>P</i>	0.0006	0.0317	<0.0001	



**Table 6.8.** Summary of relationships between pigment concentrations and UVB, UVPE, temperature at the surface and mixing depth for L302S in 1999. Simple linear regression analysis was performed using  $\log_{10}$ -transformed pigment and UVPE data. NS indicates a relationship that was found to be non significant. Where relationships were significant ( $P < 0.05$ ),  $r^2$ ,  $P$  value, and in parenthesis the direction of the relationship (+ = positive and - = negative) are shown.

Pigment	UVB ( $\text{kJ m}^{-2} \text{d}^{-1}$ )	Log UVPE ( $\text{J m}^{-2}$ ) <sup>2</sup>	Temp. ( $^{\circ}\text{C}$ )	Mixing Depth (m)
<b><u>Chlorophylls</u></b>				
Chl <i>a</i>	(-)	(-)	(-)	NS
$r^2$	0.48	0.16	0.48	
$P$	<0.0001	0.0009	<0.0001	
Chl <i>b</i>	NS	(-)	NS	NS
$r^2$		0.12		
$P$		0.0049		
Chl <i>c1</i>	(-)	(-)	(-)	NS
$r^2$	0.44	0.10	0.60	
$P$	<0.0001	0.0092	<0.0001	
Chl <i>c2</i>	(-)	(-)	(-)	NS
$r^2$	0.36	0.10	0.60	
$P$	<0.0001	0.0354	<0.0001	
Pheophytin <i>a</i>	(-)	(-)	(-)	(+)
$r^2$	0.32	0.18	0.36	0.16
$P$	<0.0001	0.0004	<0.0001	0.0009
Pheophytin <i>b</i>	(-)	(-)	(-)	(+)
$r^2$	0.21	0.18	0.16	0.18
$P$	0.0001	0.0004	0.0008	0.0004
<b><u>Carotenoids</u></b>				
Alloxanthin	(-)	(-)	(-)	(+)
$r^2$	0.33	0.14	0.35	0.18
$P$	<0.0001	0.0022	<0.0001	0.0005
Canthaxanthin	NS	NS	NS	NS
Diadinoxanthin	(-)	(-)	(-)	NS
$r^2$	0.31	0.12	0.21	
$P$	<0.0001	0.0047	0.0001	
Diatoxanthin	(-)	(-)	(-)	(+)
$r^2$	0.29	0.10	0.32	0.10
$P$	<0.0001	0.0148	<0.0001	0.0254
Fucoxanthin	(-)	(-)	(-)	(+)
$r^2$	0.53	0.35	0.49	0.10
$P$	<0.0001	<0.0001	<0.0001	0.0308
Lutein-zeaxanthin	NS	(-)	NS	NS
$r^2$		0.14		
$P$		0.0019		
Myxoxanthophyll	(-)	NS	(-)	(+)
$r^2$	0.16		0.17	0.10
$P$	0.0011		0.0008	0.0424
Violaxanthin	(-)	(-)	(-)	NS
$r^2$	0.30	0.10	0.16	
$P$	<0.0001	0.0106	0.0010	
$\beta$ -carotene	(-)	(-)	NS	(+)
$r^2$	0.16	0.10		0.11
$P$	0.0009	0.0129		0.0080
<b><u>Grazing pigment</u></b>				
Pheophorbide	NS	NS	NS	NS



**Table 6.8.** Continued.

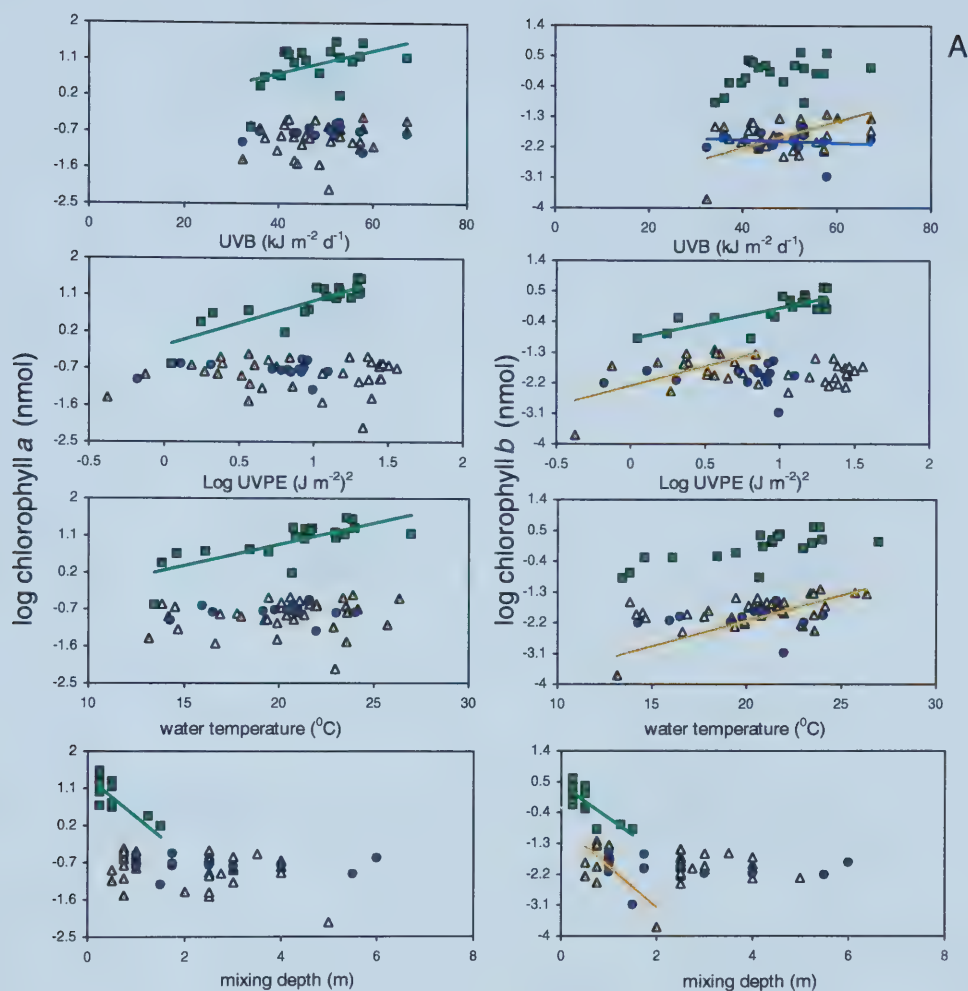
<u>Ratios and Totals</u>				
Chl <i>a</i> :fucoxanthin	NS	(+)	NS	NS
$r^2$		0.12		
<i>P</i>		0.0059		
Chl <i>a</i> :lutein-zeaxanthin	(-)	NS	(-)	NS
$r^2$	0.39		0.54	
<i>P</i>	<0.0001		<0.0001	
Total carotenoids	(-)	(-)	(+)	(+)
$r^2$	0.50	0.28	0.47	0.10
<i>P</i>	<0.0001	<0.0001	<0.0001	0.0209
Chl <i>a</i> : tot. carotenoids	(-)	NS	(-)	NS
$r^2$	0.10		0.16	
<i>P</i>	0.0140		0.0009	
Total chlorophylls	(-)	(-)	(-)	NS
$r^2$	0.51	0.13	0.66	
<i>P</i>	<0.0001	0.0033	<0.0001	





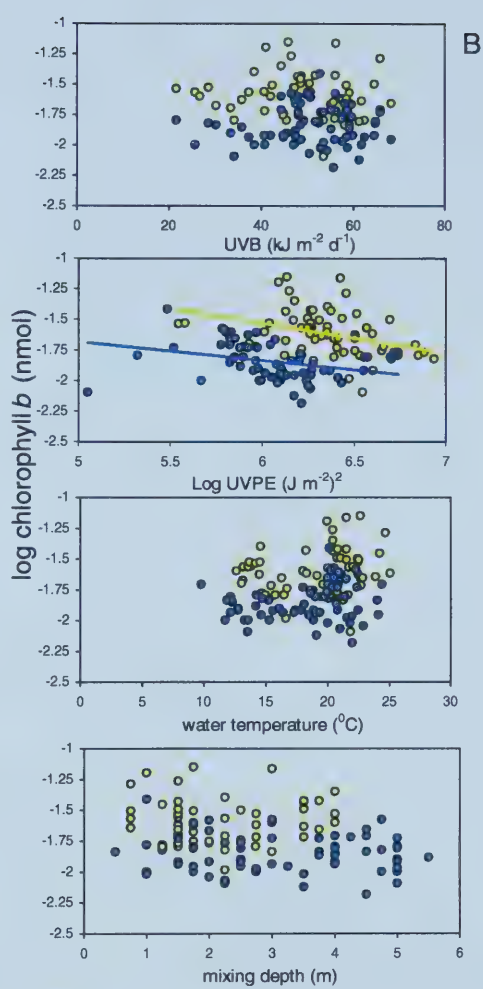
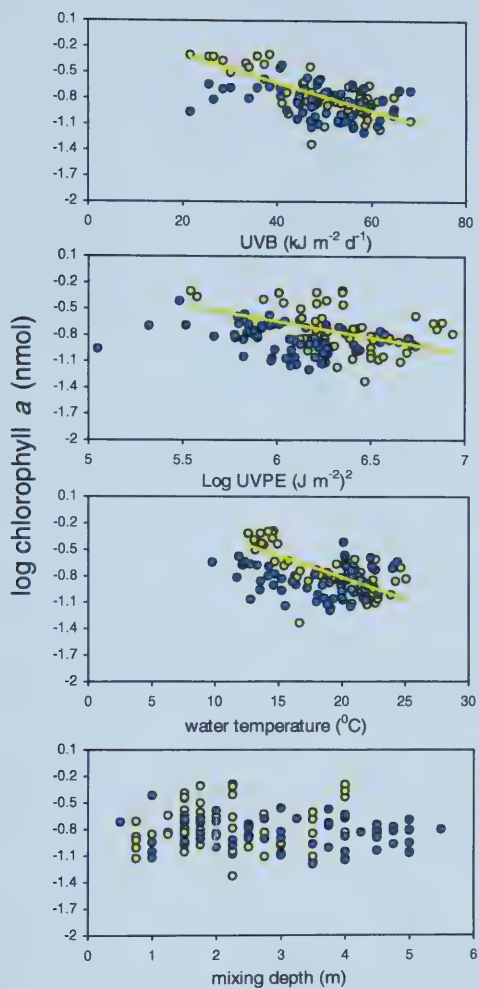


**Figure 6.3.** Relationships between chl *a* and *b* and environmental variables (UVB, UVPE, temperature and mixing depth) in a) 1998 and b) 1999. Regression lines are only shown where the slope was found to be significant ( $P < 0.05$ ).



△ L305    ● L224    ■ L227    ▲ L225



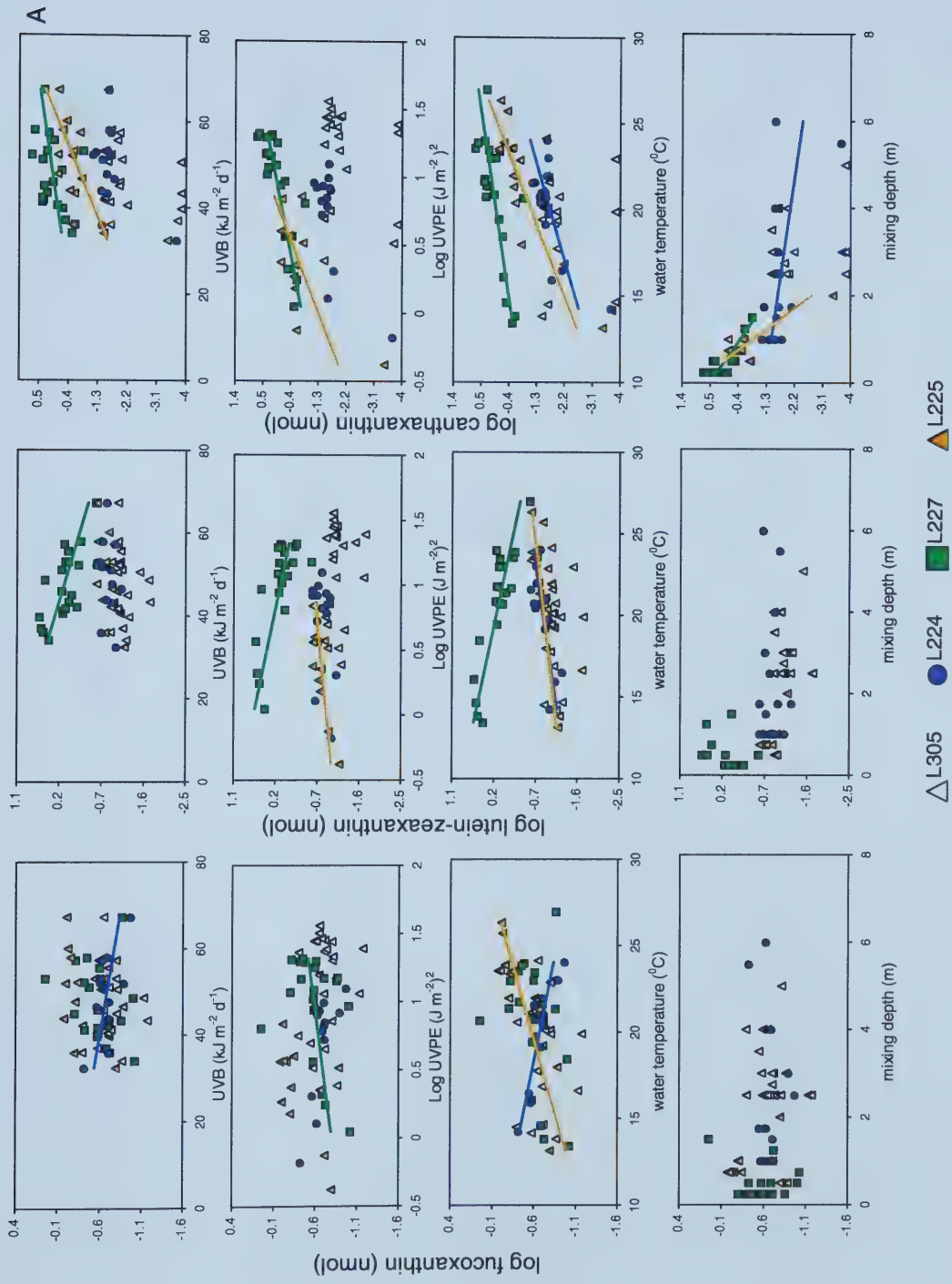


B



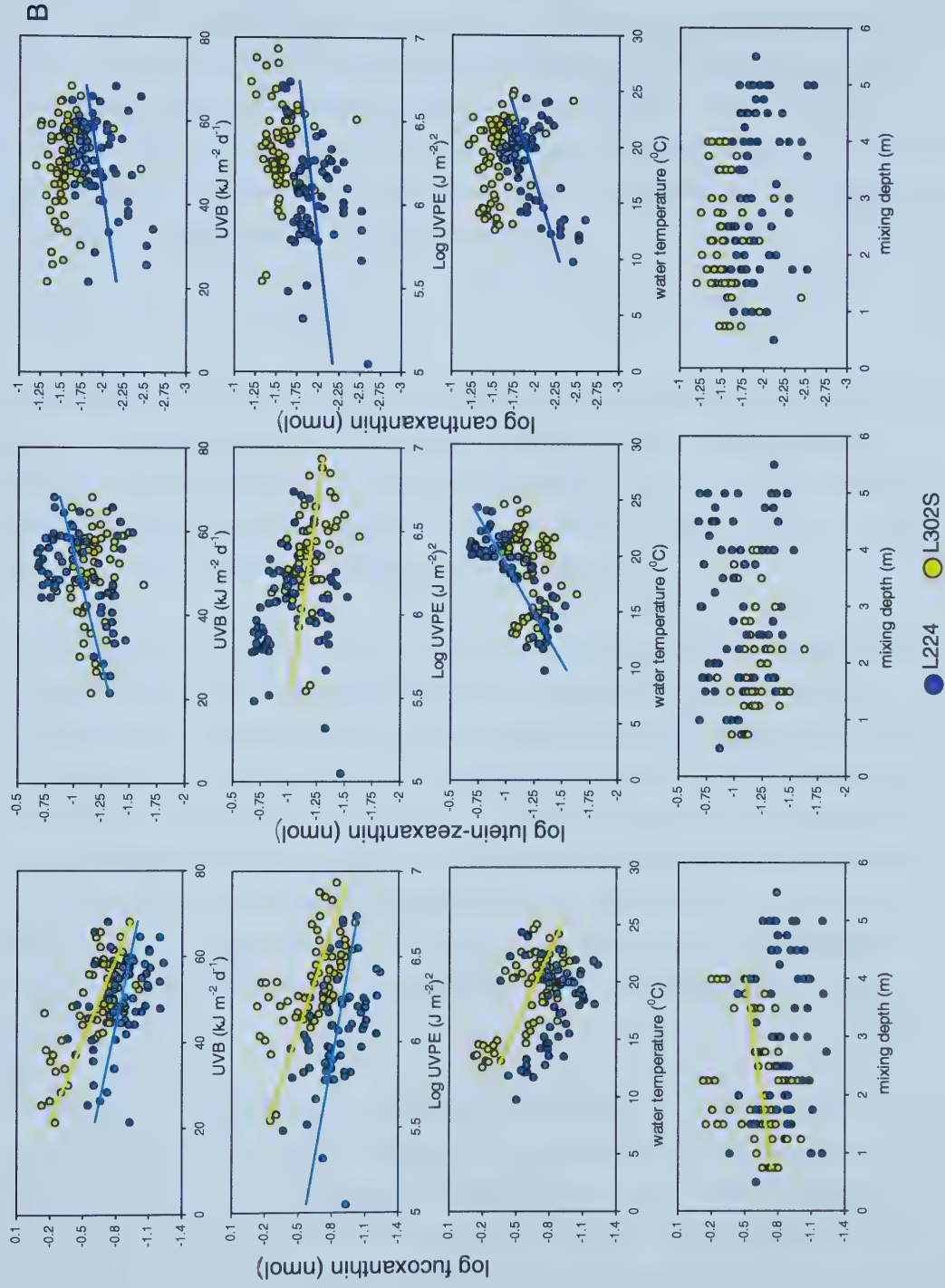


**Figure 6.4.** Relationships between three major carotenoids (Fucoxanthin, lutein-zeaxanthin and canthaxanthin) and environmental variables (UVB, UVPE, temperature and mixing depth in a) 1998 and b) 1999. Regression lines are only shown where the slope was found to be significant ( $P < 0.05$ ).











## DISCUSSION

Phytoplankton pigments were variable in their responses to physical factors in our study. Nevertheless, several generalizations about the role of UVR in lake ecosystems can be made. First, differential sensitivity to UVR was observed between chromophytes, Cyanobacteria and dinoflagellates. Cyanobacteria and dinoflagellates respond positively to high UVR and chromophytes respond negatively or not at all. Second, phytoplankton responses to UVR, mixing and temperature in this study differed among the study lakes. Below, we examine the likely causes of these trends and how they compare to other studies.

### Taxonomic responses to UVR

Dinoflagellates and Cyanobacteria increase in surface waters during high irradiances. On the other hand, diatoms and chrysophytes are more sensitive (but not always) to damage from UVR. Reduced pigment concentrations of diatoms and chrysophytes at high UV may be a consequence of their relatively high sinking rates (Burns and Rosa 1980; Harrison et al. 1986; Granata 1991; Neale et al. 1991) compared with non-siliceous or motile species.

For dinoflagellates, slow sinking rates may allow them to proliferate near the surface, especially during pronounced stratified conditions. We found a negative relationship between the tracer pigment peridinin and the depth of the mixed layer (Table 6.5) in L225. Juhl et al. (2001) found that the dinoflagellate *Alexandrium* had reduced growth rates under turbulent conditions. High concentrations of dinoflagellates near lake surface waters have been previously documented (Nielsen and Ekelund 1993; Riegman and Kraay 2001; Xenopoulos et al. 2000). Acidification caused increased transparency to UVB which led to greater abundances of dinoflagellates in L302S (Leavitt et al. 1999). The reason for the increase in dinoflagellates in high irradiances is likely related to their relatively high photoprotective capabilities (via pigments (MAAs), Carreto et al. 1990).

Cyanobacteria, which are the primary taxonomic group in eutrophic L227, were more abundant (in biomass) at high irradiances in the surface waters. This increase in Cyanobacteria (via canthaxanthin) was also observed in lakes 225 and 224 (only in 1999). Some Cyanobacteria produce photoprotective pigments (e.g. scytonemin; Garcia-Pichel and Castenholz 1991). We found high concentrations of a photoprotective pigment with similar properties to scytonemin in



L227. Cyanobacteria are resistant to UVB damage, presumably because they have low ratios of chlorophyll:carotenoids which is indicative of UV protection. The increase in carotenoids may be especially important in brightly illuminated environments particularly near surface waters (Paerl et al. 1983; Roy 2000). Opposite to what we expected, algae in L227 contained higher amounts of chlorophyll relative to carotenoids under high irradiance conditions (Table 6.6). The increase in chlorophyll *a*, *b* and *c* at high irradiance and low mixing was also unexpected (Table 6.6). This may be due to light limitation by algal cells in this lake (see below). Photosynthesis was also stimulated by UVB in this lake (Hazewinkel, Xenopoulos and Schindler, unpublished data). On the other hand, some Cyanobacteria did not increase in biomass with increased UVB. Filamentous or colonial Cyanobacteria (myxoxanthophyll) were negatively related to high irradiances in L227 and L302S. This variable sensitivity to UVR within an algal group has previously been found (Xiong et al. 1997).

Diatoms and chrysophytes were generally unaffected by increasing irradiances except in L224 and L302S where they were negatively affected. Unfortunately, our survey cannot determine if diatoms and chrysophytes are damaged by UVR or are simply sinking out of the surface waters (Neale et al. 1991). We did not find an increase of chromophytic-related pigments in the bottom of the mixed layer on days with high UVB and low mixing (results not shown). Nevertheless, detailed studies of growth and losses simultaneously at different water layers will be needed to assess the role of sinking in mediating UV responses. Sinking can be viewed as a potential defense mechanism against UVR damage in susceptible algal taxa. How ubiquitous such responses are and how they vary among taxa remain topics that need to be addressed.

### **Inter-lake responses to UVR**

The dark (high DOC) and nutrient-rich lakes in our study generally had positive relationships between pigment and surface irradiance, particularly under restricted mixing conditions. Phytoplankton from both L227 and L225 are severely light limited due to limited penetration of light into their water columns. It seems that in these lakes, growth stimulated by high PAR exceeds damage from high UVB and UVA. The balance between damage, repair and growth resulted in an overall increase in biomass during high light days, causing the positive relationships between pigments and irradiance that we found.





In contrast, we found few relationships (positive or negative) between pigments and irradiance in transparent (low DOC), oligotrophic lakes. Perhaps phytoplankton in these lakes are adapted to high light and not susceptible to its damage. Species in these lakes have evolved in conditions of high light and may have adaptations that reduce physiological damage to UVR (Frost and Xenopoulos, unpublished data). In addition, low phytoplankton biomass ( $\sim 1 \mu\text{g L}^{-1}$ ) is typical for lakes 224 and 305, a result of chronically low nutrient concentration. Consequently, the biomass of phytoplankton in these oligotrophic lakes does not vary as much as their counterparts in eutrophic lakes such as L227. Nutrients are probably more important than UV in structuring the phytoplankton communities in oligotrophic lakes. Little UVB inhibition of phytoplankton growth in L224 was found at ambient phosphorus levels (Xenopoulos et al. in press). Only when phosphorus was added did UVR damage become apparent (Xenopoulos et al. in press). This co-regulation has far-reaching consequences at large scales. Global changes are being seen in the biogeochemical cycles of N and P (Vitousek et al. 1997; Falkowski et al. 2000; Tilman et al. 2001) and as a result, the deposition of important nutrients (nitrogen and phosphorus) is increasing. This might also increase the likelihood that UVR damage will be observed in these lakes.

We also found the highest UVR sensitivity in Lake 302S, which contains slightly higher concentrations of nutrients and is darker than L305 and L224 (see Table 6.2). Sensitivity to UVR in mesohumic lakes has been recorded in other studies (e.g. Xenopoulos et al. 2000; Kaczmarek et al. 2000). It is usually attributed to shallower mixed layers. However, in L302S, the relationships explained by mixing depth or UVR  $\times$  mixing (UVPE) were either not significant or explained little variation (Table 6.8).

Lakes like L302S may be particularly vulnerable to an increase in UVB exposure because the DOC levels in these lakes are in the lower range ( $4\text{--}5 \text{ mg C L}^{-1}$ ). Climate warming and lake acidification will reduce the DOC concentration (Schindler et al. 1996; Donahue et al. 1998; Yan et al. 1996) to what may be dangerously low levels. Below a concentration of  $\sim 3 \text{ mg C L}^{-1}$ , UVR penetration increases exponentially (Schindler et al. 1996). Indeed, this rapid increase in transparency was observed after the artificial acidification of L302S (1989–1991).





## Grazing responses to UVR

Reduced grazing (indicated by pheophorbide) at high irradiances and temperatures occurred in our transparent lakes. Lower concentrations of this pigment could result from grazers avoiding the photic zone during times of high irradiances (Speckmann et al. 2000). In particular, the grazer *Daphnia* has been found to migrate downwards when exposed to UVB (Leech and Williamson 2001; Rhode et al. 2001). Alternatively, high UVB may directly damage grazers (Leech and Williamson 2000; Zagarese and Williamson 2000) and reduce their excretion of this pigment. Further experiments are needed to determine how planktonic grazers and their interaction with phytoplankton will change under high irradiances, as has been shown for attached algae and their grazers (Bothwell et al. 1994).

## Temperature

Water temperature explained more variance in pigment concentrations than UVB or UVPE. Interactions of UVB and temperature in lake ecosystems are still poorly understood. In organisms, UV-repair processes are dependent on temperature (Aráoz et al. 1998; Kulandaivelu and Nedunchezian 1993; Pakker et al. 2000; Roos and Vincent 1998), as enzyme activity increases at warm temperature. It follows that UVR resistant taxa would be positively related to temperature. Cyanobacteria (via canthaxanthin) and often chlorophytes (via lutein-zeaxanthin) increased with temperature in our study lakes. In contrast, we found that most chromophytic pigments (diatoms and chrysophytes) were negatively related to temperature. The negative relationship between temperature and these pigment could results from increased entrainment of algae or nutrients from the metalimnion during time of cooler surface temperatures which would increase nutrients in the water column and favor algal growth (Fee 1976). Chrysophytes and diatoms are generally associated with lower growth at reduced nutrient concentrations (Grover 1989; Tilman et al. 1986). We suspect that nutrient limitation and temperature play a greater role than UV-damage in structuring the phytoplankton communities in these lakes. This has also been shown for microbial communities in Northern Quebec (Bergeron and Vincent 1997; Rae and Vincent 1998)

## Ratios

The response of chl:carotenoid ratios of UVB exposed phytoplankton was variable. These ratios appear to be poor indicators of physiological adaptation to light in these lakes. On occasion

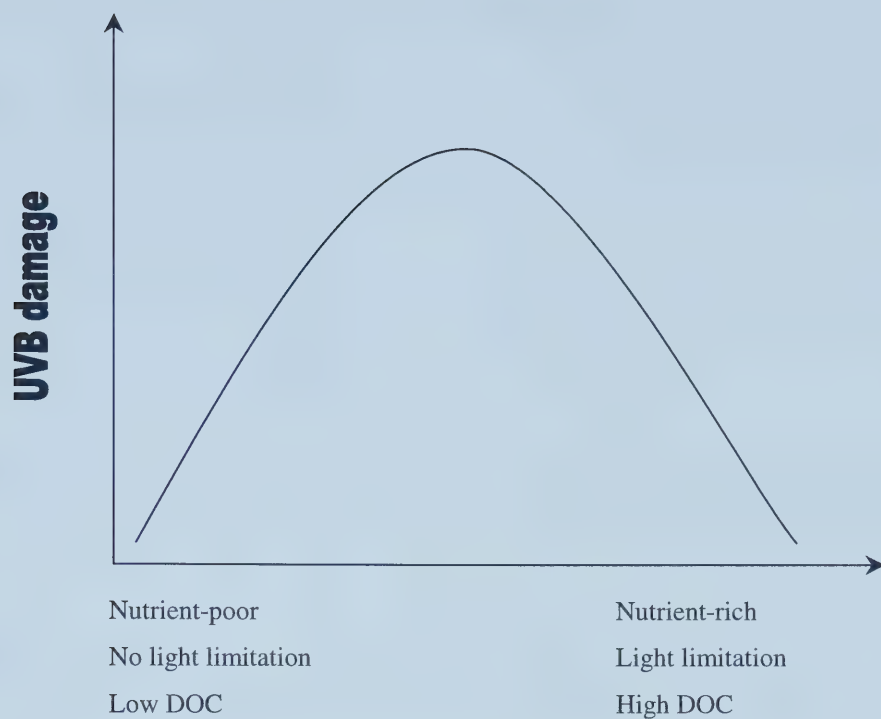


pigment ratios changed in the direction we expected, but changes were usually not significant. Although we only use fucoxanthin and lutein-zeaxanthin for our ratios in this paper, we found our conclusions to be the same with the other carotenoids. In these lakes, carotenoids may be better indicators of biomass than physiological adaptation at the scale we have measured them.

## Conclusions

Although UVR, particularly under restricted mixing, can have an effect on lake ecosystems, this effect is not always negative. As lakes increase in nutrient concentration their sensitivity to UVR increases but then declines again as light become limiting at high algal biomass (Fig. 6.5). Our results generated this conceptual model of UV effects from lakes varying in light and nutrients. Although still speculative, this model demonstrates that considerations of whole ecosystem processes such as mixing, succession, grazing, nutrients and temperature are clearly important when examining ecological processes. Additional data are needed from several types of lakes to determine which will be the most sensitive to increases from UVR from stratospheric ozone depletion or increases in UVR penetration from climate warming. Ecosystem experiments combine mixing processes, all biological interactions within the system and large-scale geochemical processes (Schindler 1998). This information is needed to accurately assess UVR effects on whole lake ecosystems.





**Figure 6.5.** Conceptual diagram of how UVR damage may influence lakes of different trophic state and transparency.



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## 7. GENERAL CONCLUSIONS

### Ultraviolet radiation and global change

Future global change (altered land use, eutrophication, over-fishing, acidification, introduction of exotic species, climate change, ultraviolet radiation and other human-induced changes) threatens the healthy functioning of aquatic ecosystems. A few studies have shown that the cumulative effects of several factors can act synergistically (see special issue on multiple stressors: Breitburg et al. 1999). These interactions can have effects that are greater than or different from the studies that consider one factor at a time. However, the scarcity of studies on the complex interactions between many of these factors limits our ability to forecast and alleviate serious environmental degradation. For example, interactions among climate warming, drought, and acidification can cause significant declines in concentrations of dissolved organic carbon in lakes, which in turn increases ultraviolet radiation (UVR) penetration (Schindler et al. 1996; Yan et al. 1996; Donahue et al. 1998). Here, I examined the effects of UVR penetration combined with other ecosystem processes such as reduced mixing, nutrients inputs and succession on the plankton of boreal lakes, especially in near-surface waters. The interactions between these multiple factors have been ignored at smaller scales.

### In summary...

In chapter 2, I reviewed the ubiquity of UVR in the environment and show how its flux is a function of several factors some of which are modified by anthropogenic activity. Near-surface thermoclines are especially common in small lakes but occur frequently even in large lakes. The incidence of transient thermoclines decreases with increasing lake size from 90% of all summer days in small lakes (< 4 ha) to 40% or less in > 100 ha (chapter 3). The frequency of near-surface thermoclines also declines with increasing wind speed and water transparency (chapter 3). Near surface thermoclines can trap sensitive phytoplankton (e.g. Vincent et al. 1984). However, these 'traps' may or may not increase UVR damage to phytoplankton depending on the lake (chapter 6), phytoplankton taxa (chapter 6), nutrient concentration (chapter 4), time of the year (chapter 4) and light  $\times$  stratification history of the cell (chapter 5). Phytoplankton exposed to high levels of UVA and UVB in these shallow thermoclines can have reduced biomass, growth rates, photosynthesis and sestonic C:P ratios but not always.



## Is UVR a major factor shaping boreal lake communities?

The importance of UVR and its interaction with near-surface thermoclines in structuring phytoplankton communities, when incorporating ecosystem processes (mixing, succession, adaptation, temperature and nutrient supply), is not as significant as isolated small-scale, static experiments with a single taxa or factor have shown (e.g. Milot-Roy and Vincent 1994; Bergeron and Vincent 1997). Even though near-surface thermoclines are common, their general influence of UVR on lakes is not as dramatic as early UVR studies predicted. For instance, I showed that food quality for zooplankton increases after UVR exposure (chapter 4). I also showed that oligotrophic, transparent lakes are not as sensitive to UVR exposure (chapter 6) as many would assume. Planktonic organisms in these lakes may have in their physiological arsenal mechanisms to protect themselves from damaging irradiances. For example, phytoplankton may be able to sink out of the near-surface thermoclines or produce protective pigments. Further studies are needed to assess how sinking rates change under high irradiances and the extent of physiological adjustments in plankton when 'trapped' in near-surface waters (see chapter 5). Another area of potential future work is on the role evolution plays to counteract UVB effects (Cockell 2001). It is perhaps not surprising, that Cyanobacteria are better able to cope with high UVR than chromophytes (chapter 6). Historically, Cyanobacteria evolved when the ozone layer was forming. It may also not be surprising that transparent lakes (chapter 6) or periphyton (e.g. Hill et al. 1997) are unaffected by UVB. These systems have also evolved to produce resistant species.

Many properties of ecosystems cannot be studied at smaller scales (e.g. mixing). Under natural conditions, I showed that reduced mixing and shallow thermoclines do not always exacerbate UVB damage (chapter 6). Some species (such as Cyanobacteria and dinoflagellates) may even increase under shallow stratification and high irradiance because the presence of high PAR likely offsets damage induced by high UVR (Vernet 2000). This illustrates the importance of considering whole ecosystem processes to better predict how lakes or biodiversity will respond to anthropogenic stressors. While individual taxa can be affected by a stressor, others come to replace them (Schindler 1987, 1990). Small-scale experiments using optical screens are useful for isolating the effects of the specific wavelengths, however they create unrealistic conditions and may actually overestimate UVB damage (Schindler 1998, see review by Vernet 2000). These smaller scale experiments can give results that are spurious in a whole ecosystem setting (Schindler 1998). As a result, future UVR studies should consider using whole ecosystem settings. Tools such as temperature gradient microprofilers (e.g. Self-Contained Autonomous



Microprofiler, SCAMP-Precision Measurements Engineering, Carter and Imberger 1986) can be used to estimate the intensity and time scales of vertical mixing in the water column and extrapolate phytoplankton trajectories and the cumulative UVB radiation that these algae experience (Xenopoulos, Edwards and Culver, unpublished data).

Williamson et al. (2001) recently showed that UVR is an important factor for structuring zooplankton communities in Alaskan lakes across a chronosequence. However, it seems that UVR alone is not the factor shaping boreal lake communities but instead interacts with other important physical and chemical factors. For example, in chapter 4, I showed that UVB damage is generally only apparent when high concentrations of phosphorus are present. I also showed that the 'UVB damage signal' is dampened by the many other factors (e.g. grazing, mixing, nutrients) that interact simultaneously to form lake ecosystems (chapter 6). In the end, it is the interaction between UVR and other lake physical and biological processes that are important in structuring boreal lakes. This means that future UVR studies for the boreal phytoplankton should endeavor to incorporate multiple stressors. Another potential area of future work is how UVR mediates species interactions in lakes. Interactions between multiple species may modify anticipated responses to UVR (e.g. periphyton and their grazers, Bothwell et al. 1994; bacterioplankton and phytoplankton, Sommaruga et al. 1997; Xenopoulos and Bird 1997).

In closing, ignoring ecosystem processes has reduced our ability to understand important questions about the potential increase in UVR from global change. These multiple changes will likely promote the prevalence of some aquatic taxa over others. A better acceptance of ecosystem science and its often non-experimental, non-replicated evidence by the scientific community is needed. While ecosystem-scale experiments are not very well replicated, most would agree that these experiments make important contributions and will be an essential tool of aquatic ecologists well into the future (Schindler 1998).





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